A COMPARATIVE STUDY OF INTERTIDAL SPECIES OF SPHAEROMIDAE (ISOPODA FLABELLIFERA)

A thesis presented for the degree of

Doctor of Philosophy in Zoology

in the

University of Canterbury

Christchurch, New Zealand,

by

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1968

'There are so many ways of looking at these things.'

Gerard Hoffnung.

ABSTRACT

Part I

Ecological distributions of 10 sympatric littoral species of Sphaeromidae of rocky shores, and three species of brackish waters are described. Morphological and physiological differences are compared and correlated with distributions and environmental conditions. Population studies of the rocky shore species at Kaikoura show that distribution and breeding are closely related: in several species juveniles and adults are differently distributed, the greatest differences, together with the highest reproductive capacities occurring in the species exposed to the greatest wave action.

Part II

Geographic and seasonal variation in frequencies of colour forms of Isocladus armatus correlate with environmental differences in temperature; in the laboratory, colour forms showed differences in tolerance of temperature and salinity.

CONTENTS

INTRODUCTION

Ecological information about Sphaeromidae is either very general, as in Menzies (1962): 'The Zoogeography, Ecology, and Systematics of the Chilean Marine Isopods', or detailed, as in studies of Sphaeroma hookeri in Kiel Harbour (Kinne, 1954), and Copenhagen Harbour (Jensen, 1955). In New Zealand, the scattered ecological notes on Sphaeromidae were gathered by Hurley (1961) in 'A Checklist and Key to the Crustacea Isopoda of New Zealand and the Subantarctic Islands'.

In the first part of the present study, ecological distributions and adaptations of ten sympatric rocky shore species of Sphaeromidae, and three brackish water species, are examined and compared.

In the second part, the means by which allopatric species populations are adapted to different local conditions are considered. The problem can be stated: 'Are allopatric species populations adapted by all individuals adjusting to local conditions, or by providing a variety of phenotypes, of which the less adaptive in each locality die off?' (see Bullock, 1958; Kinne, 1963, 1964). Geographic and seasonal variations in frequencies of colour forms of Isocladus armatus in New Zealand are examined in relation to environmental differences, and tolerances of temperature and salinity.

Characteristics of the family

Sphaeromidae are a family of the Tribe Flabellifera of the Order Isopoda. There are seven pereonal (thoracic) segments and pairs of pereopods (thoracic legs) in adults, but only six in newly released young. The pleon (abdomen) comprises two distinct segments: the anterior supports five pairs of biramous pleopods ventrally; the terminal telson carries biramous uropods attached antero-laterally, the inner rami being fixed but the outer movable. The name Sphaeromidae is derived from the habit of rolling the body into a nearly spherical shape (Greek 'sphaera' a pill or sphere).

External morphology

The body is divided into cephalon (head), pereon (thorax), and pleon (abdomen). Maximum overall length (from the anterior margin of the cephalon to the posterior tip of the telson) in the species studied ranges from 4.5 mm in Cymodocella tubicauda (Fig. 8) to 17 mm in Exosphaeroma obtusa (Fig. 6); width is about one half the length. Shape and surface vary from dorso-ventrally flattened and smooth (Amphoroidea falcifer, Fig. 14) to deep and sculptured (Dynamenopsis varicolor, Fig. 10). Colour is always cryptic, varying within and among species.

The cephalon is usually slightly narrower and longer than

the first pereonal segment. The anterior margin often projects in a small apex, below and either side of which the shorter first and longer second antennae are inserted. The eyes are well developed, set laterally on the cephalon, and face forward, outward and upward. Between the bases of the antennae the epistome faces antero-ventrally and extends posteriorly to the labrum which partly covers the anterior part of the mandibles and mouth opening (Fig. 4). The mandibles (Fig. 3) are well developed, with palps, and are asymmetrical, recorded also in Idotea (Isopoda Valvifera) by Naylor (1955c); the incisor processes, laciniae mobiles, and molar processes vary among the species (see Ecological Adaptations). First and second maxillae and maxillipeds lie ventral and posterior to the mouth opening and paragnath (Fig. 4).

The pereon comprises seven segments contained by sclerotised tergites, laterally fused coxal plates, and unsclerotised sternites. A pair of pereopods corresponds with each pereonal segment. Each pereopod comprises six movable articles, the coxae being fused laterally with the tergites and sternites, and ends in a claw (dactylos) and a short stout spine. Among the species the pereopods vary in antero-posterior differentiation, in development of the claws, and in the armature of spines, blades, and hairs (see Ecological Adaptations).

The pleon comprises two segments and their appendages.

The single pre-telsonic segment appears to arise from fusion of five somites as it supports five pairs of biramous pleopods: the first three pairs, used in swimming, are lightly sclerotised and bordered with long setae; the last two pairs, presumably respiratory, are unsclerotised and without setae. The rami of the last two pairs of pleopods appear in two forms: thin with flat surfaces, or fleshy with plicate surfaces, variously combined in the three groups of genera into which the family is divided (Hansen,1905). The body ends posteriorly in the telson which carries the biramous uropods.

Sexual differentiation

Sexual differences are not apparent in small specimens but develop with growth. Males tend to be larger than females and in several species are more prominently sculptured (Figs. 3-17).

In males, paired penes originate behind the seventh pereonal sternite, and appendices masculinae (Fig. 4) from the inner margins of the inner rami of the second pleopods.

In females, paired oostegites (Fig. 5) originate from the inner bases of the fused coxae of the second, third, and fourth pereopods; paired oviducts open in the fifth pereonal sternite (Fig. 5). (Metamorphosis of mouth-parts (Hansen, 1905) does not occur in gravid females of the genera included in this study.)

Life cycles

Reproduction and embryonic development

Females are first recognisable externally by rudimentary oostegites (Fig. 5); when these appear the ovaries are full of large yolky eggs. Following the subsequent moult the eggs remain in the ovaries but rudimentary brood sacs appear (Fig. 5); the oostegites are either unchanged or now fully developed, apparently depending on whether copulation has occurred (Jensen, 1955). After a further moult, following copulation, the oostegites are fully developed in all cases and the eggs have been transferred from the ovaries to the internal brood sacs, presumably fertilised as they pass down the oviducts. The brood sacs are now distended by the eggs so that they occupy nearly the whole body cavity, packed around the gut and extending into the cephalon and pleon.

The embryos develop through a sequence of stages (Fig. 5). Initially the eggs are rounded and yolky; in the second stage, elongation and segmentation have begun; in the third stage rudimentary appendages are visible and the yolk is further reduced; in the fourth stage the embryos are larger with less yolk and clearly recognisable as miniature isopods with distinct eyes, segments and appendages; in the fifth and final stage the yolk has disappeared and the embryos are lightly pigmented; the segments and appendages are fully developed except that the seventh pereonal segment is very

small and overlapped by the sixth, and the seventh pereopods have not appeared (see also Kinne, 1954).

In this form the embryos squeeze out from the brood sacs, remain beneath the oostegites or clinging to the female for a variable number of hours and finally swim free as post-embryonic juveniles. The whole brood may take up to three days to hatch (from laboratory observations of Isocladus armatus, Exosphaeroma obtusa, Dynamenella huttoni).

Post-embryonic development

Development of the seventh pereonal segment and pereopods continues through the first four stadia, being complete after the fourth moult. Growth continues with each subsequent moult with no other external changes until the sexual characters appear. Seasonal variations in mean length of juveniles, males, and females indicate seasonal variation in the number of stadia spent as pre-adult juveniles (see 'Breeding Populations').

Adult development

Males are first distinguishable externally by the penes which appear as tiny rudiments at the posterior margin of the seventh pereonal sternite and grow with each succeeding moult. At the same time the appendices masculinae (Fig. 4) appear at the inner distal ends of the inner rami of the second pleopods as small projections which separate toward the bases of the rami progressively with succeeding moults.

Concurrently the testes grow and the body changes toward the distinctive male form, differences from the female form increasing with each moult.

Females are first distinguishable by the oostegites which appear as small projections from the sternites, medial to the fused coxae of each of the second, third, and fourth pairs of pereopods (Fig. 5). Females are presumed to be mature at this stage as copulation takes place regardless of the size.

Gravid females and mature males as well as post-embryonic and pre-adult juveniles were effectively present throughout the year in all the species studied at Kaikoura, indicating protracted or continuous breeding. A general trend toward lower mean lengths of males and females together with higher proportions of post-embryonic juveniles indicates that both development and breeding are accelerated during the warmer summer months (see 'Breeding Populations').

Rate of Growth

Since post-embryonic juveniles were present throughout the year, it was not possible to estimate the rate of growth from the monthly samples. Young of Exosphaeroma obtusa and Isocladus armatus hatched in the laboratory survived for several weeks during which the observations recorded in Table 1 were made.

Table 1. Rate of growth during early stadia in *Exosphaeroma obtusa* and *Isocladus armatus*.

Stadium	1	2	3	4	5	6
E. obtusa						
Mean length, mm	1.6	2.0	2.4	3.2	3.8	4.4
Average duration, days	18	16	23			
I. armatus						
Mean length, mm	1.6	1.9	2.3	2.9		
Average duration, days	20	15	19			

Mortality increased after the third stadium and lengths in both species became so varied that stadia could not be separated with certainty. Laboratory conditions were not controlled and in any case bear little relation to changing field conditions. Tentative extrapolation from these data leads to the conclusion that in these species the sizes at which sexual maturity and breeding activity were observed in field populations (see 'Breeding Populations') would be reached in four to five months from hatching.

Longevity

There is no direct evidence regarding longevity. There are however indications that the life span does not significantly exceed a year (see also Kinne, 1954; Jensen, 1955; Naylor, 1955b). After summer peaks in breeding in most species the numbers of large males and females decline. At the same time the exoskeleton of the largest survivors becomes very dull and eroded, and the incisor processes of the mandibles chipped and broken, which may indicate a breakdown in the moulting process related to the preceding reproductive activity.

Feeding and diet

Functioning of sphaeromid mouthparts agrees with the description of Idotea (Isopoda Valvifera) by Naylor (1955c):

the mouthparts (Figs 3, 4) work metachronally. Strong distal spines on the endites of the maxillipeds and first maxillae together with the incisor processes of the mandible scrape and tear food into small particles. Food particles separated by the maxillipeds and first maxillae are passed to the incisor processes and lifted by the laciniae mobiles to the molar processes. Food is triturated between the serrated surfaces of the molar processes and then drawn into the foregut. Loss of small particles is prevented by the labium and paragnath, the palps of the mandibles and maxillipeds, and by the second maxillae, broad flattened structures bordered with rows of setae.

Isopods generally are considered to be scavengers and at least potentially omnivorous, and this is true of sphaeromids; from observations of faecal pellets and gut contents, the diet of each species consists of plant and animal detritus and algal sporelings, diatoms, at least superficial cells of growing algae, and epiphytes (see 'Ecological Adaptations').

Commensals

Iais pubescens (Isopoda Asellota) was found regularly on Exosphaeroma obtusa and Isocladus armatus at Kaikoura, but on no other species. I. pubescens occurs in all stages of development on one host individual, numbers rising to

between 20 and 50 per host individual in the summer months; the commensals are much smaller than the hosts, not exceeding 3 mm in length, and crowd amongst the pereopods and costegites, occasionally on the pleopods. No disadvantage to the host is apparent.

I. californica was found similarly, on Sphaeroma quoyana only. (See also Hurley, 1956, 1961).

Other commensals occasionally observed in numbers were summer infestations of rotifers which cluster on the ventral parts of Amphoroidea falcifer and Dynamenella huttoni.

Occasionally, like other intertidal animals, sphaeromids are settled on by algal sporelings and small sessile animals: barnacles (Elminius modestus and Chamaesipho columna on Sphaeroma quoyana); tubeworms (Spirorbis on Exosphaeroma obtusa and others); large (ca. 0.5 mm long) foraminiferans (species of Allogromiidae on E. obtusa and Isocladus magellanicus).

Predators

Predation by shore fishes of several species was observed both in the laboratory and in the field; identified fish predators are:

Pseudolabrus celidotus ("spotties")

Acanthoclinus quadridactylus ("rockfish")

Tripterygion spp. ("blennies")

Trachelochismus sp. ("lumpfish")

Diplocrepis sp. ('clingfish')

Notoclinus fenestratus ('topknot')

Quantitative data are not available, but it is estimated that the combined density of the species of shore fishes reaches the vicinity of 50 m^{-2}; examination of gut contents showed that one fish of any of these species contained up to five sphaeromids of all sizes and of more than one species.

Examination of droppings of shore birds (gulls, stilts, herons, oystercatchers) did not reveal any sphaeromid remains; nor were these found in any potential invertebrate predators: anemones, flatworms, polychaetes; large anemones however accepted sphaeromids infrequently in the laboratory.

Classification

Genera of Sphaeromidae are separated into three groups as follows (Hansen, 1905):

Hemibranchiatae - pleopods 4 and 5: outer rami thin and membranous with flat surfaces; inner rami fleshy with transversely folded surfaces

Eubranchiatae - pleopods 4 and 5: outer and inner rami fleshy with transversely folded surfaces

Platybranchiatae - pleopods 4 and 5: outer and inner rami thin and membranous with flat surfaces (none included in this study).

The species studied are readily distinguishable, but there are difficulties in placing new species in a genus. In this context Menzies (1962) wrote "The one species which I refer to this genus [Dynamenella] may not belong to it . . . But I hesitate to establish another genus in this already hopelessly confused group . . ." New or doubtful species have been referred to Dr D.E. Hurley (New Zealand Oceanographic Institute, Wellington, New Zealand) who is currently revising the New Zealand Isopoda, and samples with names used in this study have been deposited with him.

Some taxonomic changes have been made and are shown in the following list of species included in this study:

Family SPHAEROMIDAE

Group HEMIBRANCHIATAE

Genus Sphaeroma Bosc

Sphaeroma quoyana Milne Edwards 1840

Genus Exosphaeroma Stebbing

Exosphaeroma obtusa (Dana 1853)

Sphaeroma obtusa Dana 1853

Genus Isocladus Miers

Isocladus armatus (Milne Edwards 1840)

Sphaeroma armata Milne Edwards 1840

Sphaeroma spinigera Dana 1853

Isocladus spiniger (Dana 1853)

Isocladus magellanicus Richardson 1906

Genus Pseudosphaeroma Chilton

Pseudosphaeroma campbellensis Chilton 1909

Group EUBRANCHIATAE

Genus Dynamenella Hutton

Dynamenella huttoni (Thomson 1878)

Dynamena huttoni Thomson 1878

Dynamenella hirsuta new species

Dynamenella cordiforaminalis (Chilton 1882)

Cymodoce cordiforaminalis Chilton 1882

Genus *Dynamenopsis* Baker

Dynamenopsis varicolor new species

Genus *Paradynamenopsis* Menzies

Paradynamenopsis crenellata new species

Genus *Cymodocella* Pfeffer

Cymodocella tubicauda Pfeffer 1881

Genus *Scutuloidea* Chilton

Scutuloidea maculata Chilton 1883

Genus *Amphoroidea* Milne Edwards

Amphoroidea falcifer Thomson 1878

KEY TO THE SPECIES INCLUDED IN THIS STUDY (Figs 3 - 17)

1. Pleopods 4 and 5: outer rami membranous and smooth, inner rami fleshy with transverse folds 2

1. Pleopods 4 and 5: both rami fleshy with transverse folds 6

2. Maxillipeds: articles of palps without lobes; pereopods 1 to 3 with long lateral setae; oostegites pass midline; outer uropodal rami coarsely serrated *Sphaeroma quoyana*

2. Maxillipeds: articles of palps lobed; pereopods without long lateral setae; oostegites short of midline 3

3. Seventh pereonal segment with backwardly directed spine in males 4

3. Seventh pereonal segment without spine in either sex 5

4. Uropods: outer rami sigmoid with pointed tips *Isocladus armatus*

4. Uropods: outer rami broad with rounded tips *Isocladus magellanicus*

5. Uropods: both rami equally developed, rather narrow, tips rounded *Exosphaeroma obtusa*

5. Uropods: outer rami about one half length of inner *Pseudosphaeroma campbellensis*

6. First antennae: first article expanded anteriorly into large plate *Amphoroidea falcifer*

6. First antennae: first article not expanded as above 7

7. Uropods: large single plates *Scutuloidea maculata*

7. Uropods: biramous 8

8. Telson without apical notch on sinus, rear margin raised *Paradynamenopsis crenellata*

8. Telson with apical notch or sinus 9

9. Surface of pleotelson smooth 10

9. Surface of pleotelson granular or tubercular 12

10. Telson: sides bent down forming tube *Cymodocella tubicauda*

10. Telson: sides not forming tube 11

11. Telson with shallow apical notch, body segments without marginal hairs *Dynamenella huttoni*

11. Telson with deep apical notch, body segments with marginal hairs *Dynamenella hirsuta*

12. Telson granular, apical sinus with median tooth in male *Dynamenella cordiforaminalis*

12. Telson very strongly tubercular, apical notch without median tooth in either sex *Dynamenopsis varicolor*

Fig. 1

The Kaikoura Peninsula; I, 'very exposed', II, 'expos III, 'semi-exposed', and IV, 'fairly sheltered' shores (after Rasmussen 1965). The wind rose is based on the numbers of days on which wind blew from the directions sho from July 1966 to June 1967; solid black represents wind of more than 10 knots; information supplied by the Kaikoura station of the New Zealand Meteorological Service The inset map of New Zealand shows the localities from which collections were made.

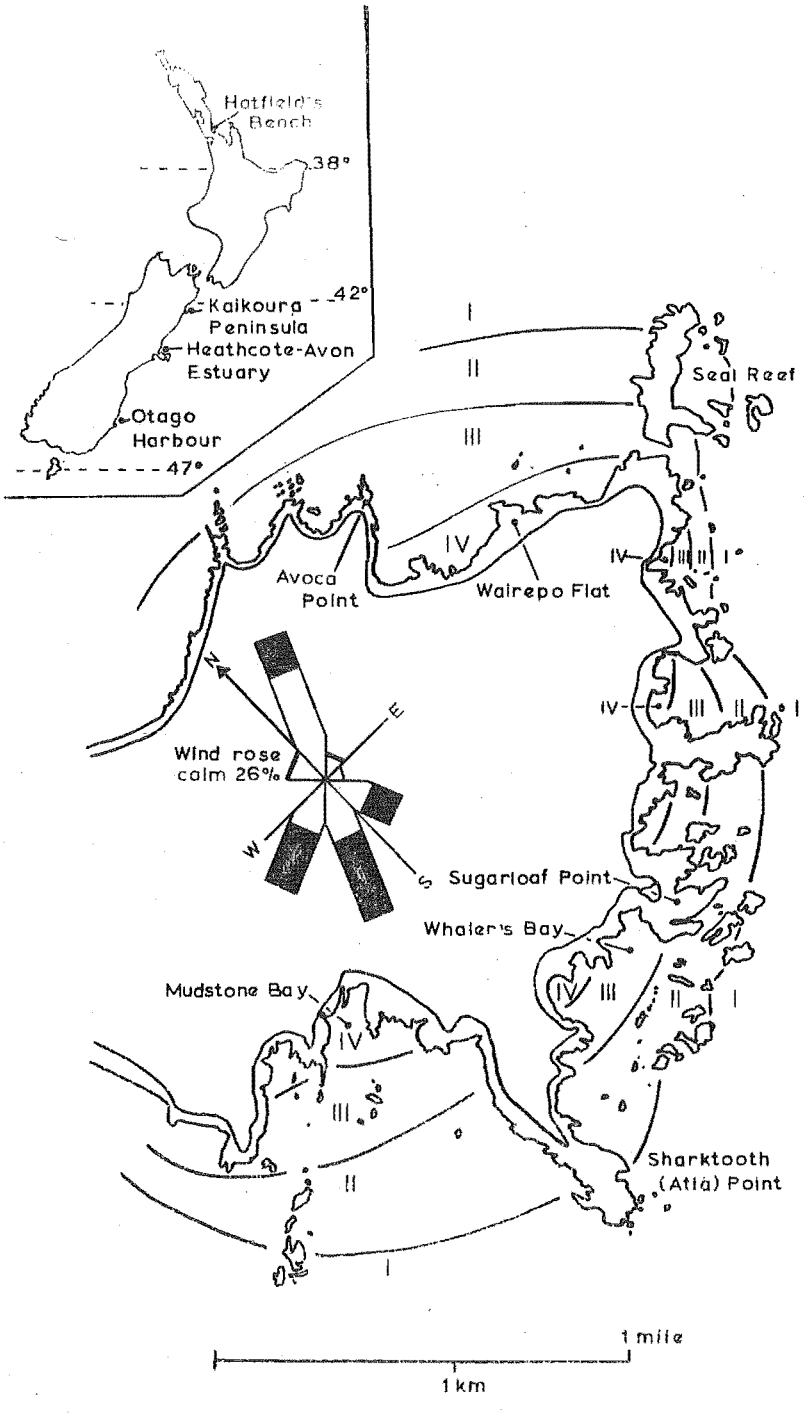

Hatfield's Beach
38°
Kaikoura Peninsula
42°
Heathcote-Avon Estuary
Otago Harbour
47°
Seal Reef
Avoca Point
Wairepo Flat
Wind rose
calm 26%
N
E
S
W
Sugarloaf Point
Whaler's Bay
Mudstone Bay
Sharktooth (Atiā) Point
I
II
III
IV
1 mile
1 km

Plate I

Class I shore, very exposed, showing wave action and substrate. Kaikoura Peninsula.

Photo J.T. Darby.

Plate II

Class I shore, very exposed, showing steep profile. Kaikoura Peninsula.

Photo J.T. Darby.

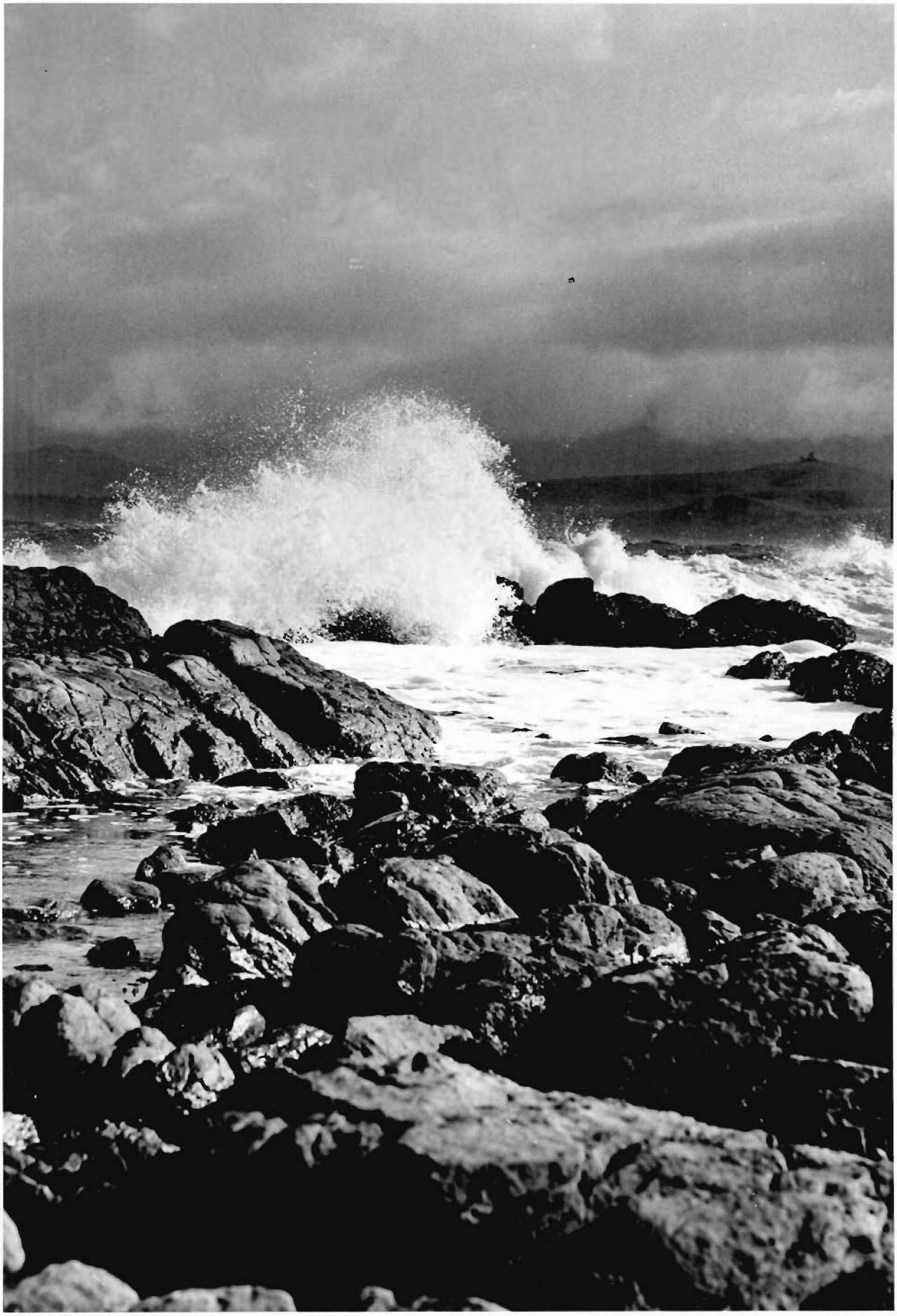


Plate III

Class II shore, exposed, showing broken profiles.
Kaikoura Peninsula.

Photo J.T. Darby.

Plate IV

Class III shore, semi-exposed, showing mixed substrates and profile. Kaikoura Peninsula.

Plate V

Class IV shore, fairly sheltered, showing flat profile. Kaikoura Peninsula.

Plate VI

Durvillea antarctica

Plate VII

Carpophyllum maschalocarpum

Plate VIII

Corallina officinalis

(beads of the 'necklace-weed' Hormosira banksii also appear)

Plate IX

Mixed sand, stones, and sandstone at MTL on a fairly sheltered shore.

ECOLOGICAL DISTRIBUTION

Rocky shore species were studied on the shores of the Kaikoura Peninsula; brackish water species were collected at Hatfield's Beach (Auckland), in the Heathcote-Avon Estuary (Christchurch), and between Dunedin and Portobello (Otago Harbour) (Fig. 1).

Materials and methods; terminology

A number of methods were used in collecting: the smallest specimens in all species are visible to the naked eye and individuals were removed with forceps from stones and algae, or large concentrations by repeated washing in sea water, in the field; small shrubby algae were examined in the laboratory under a binocular microscope.

All measurements were made of specimens freshly killed in 2% formalin, under a binocular microscope fitted with a graduated eyepiece accurate to 0.1 mm.

Because of the diversity of substrates and the extremely uneven local distributions, strictly quantitative sampling was not practicable, but all samples were taken from measured areas, in the case of algae, the area covered by the holdfasts. Relative abundances at each level on each shore were then based on average numbers per square metre and expressed in terms of the following scale:

abundant	≥ 625	m^{-2}
frequent	125 - 625	"
common	25 - 125	"
occasional	< 5 - 25	"
rare	5	"

Rocky shores of the Kaikoura Peninsula

The Kaikoura Peninsula juts two miles out from the main coastline and the shores are consequently exposed to both local and distant weather influences (Rasmussen, 1965). Rocky points extend into the sea, and while not submerged at high tides are often swept by waves or ocean swells even in locally calm weather. Bays varying in size and character lie between the points and are partly sheltered both by the points and by outlying reefs. Profiles are extremely varied so that exposure to wave action changes considerably within small areas. Substrates are diverse, comprising varying proportions of medium sand, pebbles, shingle, large stones, and solid bedrock. Algal cover changes greatly in extent and composition with wave action and substrate.

The intertidal ecology of the rocky shores of the Kaikoura Peninsula was studied by Rasmussen (1965); vertical zonation and classification of the shores on the basis of exposure to wave action (Fig. 1) are based on his work, with only minor modifications. Rasmussen pointed out the close

correspondence between his classification based on analysis of wind and wave observations and one based on Ballantine's (1961) biologically defined scale of exposure:

class I shores - very exposed

class II shores - exposed

class III shores - semi-exposed

class IV shores - fairly sheltered

CLASS I SHORES (Plates I and II)

Exposed to heavy wave action at all levels during the full tidal cycle; steep rock faces plunge into relatively deep sublittoral water; masses of smooth siltstone are separated by deep channels; loose stones and sand are sparse, confined to deep crevices.

Dominant algae: (Plates VI - VIII)

Durvillea antarctica	HWN to LWS
D. willana	HWN to LWS
Corallina officinalis	HWN to LWN
Carpophyllum maschalocarpum	below LWN
crustose corallines	below LWN

CLASS II SHORES (Plate III)

Exposed to heavy wave action at low levels during the full tidal cycle, at high levels only at high tide; profiles are irregular and sublittoral water shallower than on class I shores; masses of smooth siltstone and rough limestone stand

among expanses of large stones (diameter ca. 30 cm) lower on the shore, about LWN, and among smaller stones (diameter ca. 20 cm) with small amounts of sand above LWN; large stones are frequently overturned by wave action.

Dominant algae:	D. antarctica	MTL to LWS
	C. maschalocarpum	below LWN
	crustose corallines	below LWN
	C. officinalis	HWN to LWN

CLASS III SHORES (Plate IV)

Exposed to moderate wave action at all levels at high tide, only at the lower levels at low tide; profiles and substrates are similar to those of class II shores, but with greater proportions of smaller stones and sand at lower levels, to LWN; stones below MTL frequently overturned by wave action.

Dominant algae:	Hormosira banksii	MTL to LWN
	C. officinalis	MTL to LWN
	Cystophora spp.	below LWN

CLASS IV SHORES (Plate V)

Exposed to light wave action at all levels at high tide except in gale force winds when wave action is moderate; profiles are flat and sublittoral water very shallow; extensive platforms of smooth channelled siltstone with depressed areas filled with mixed medium sand and small stones

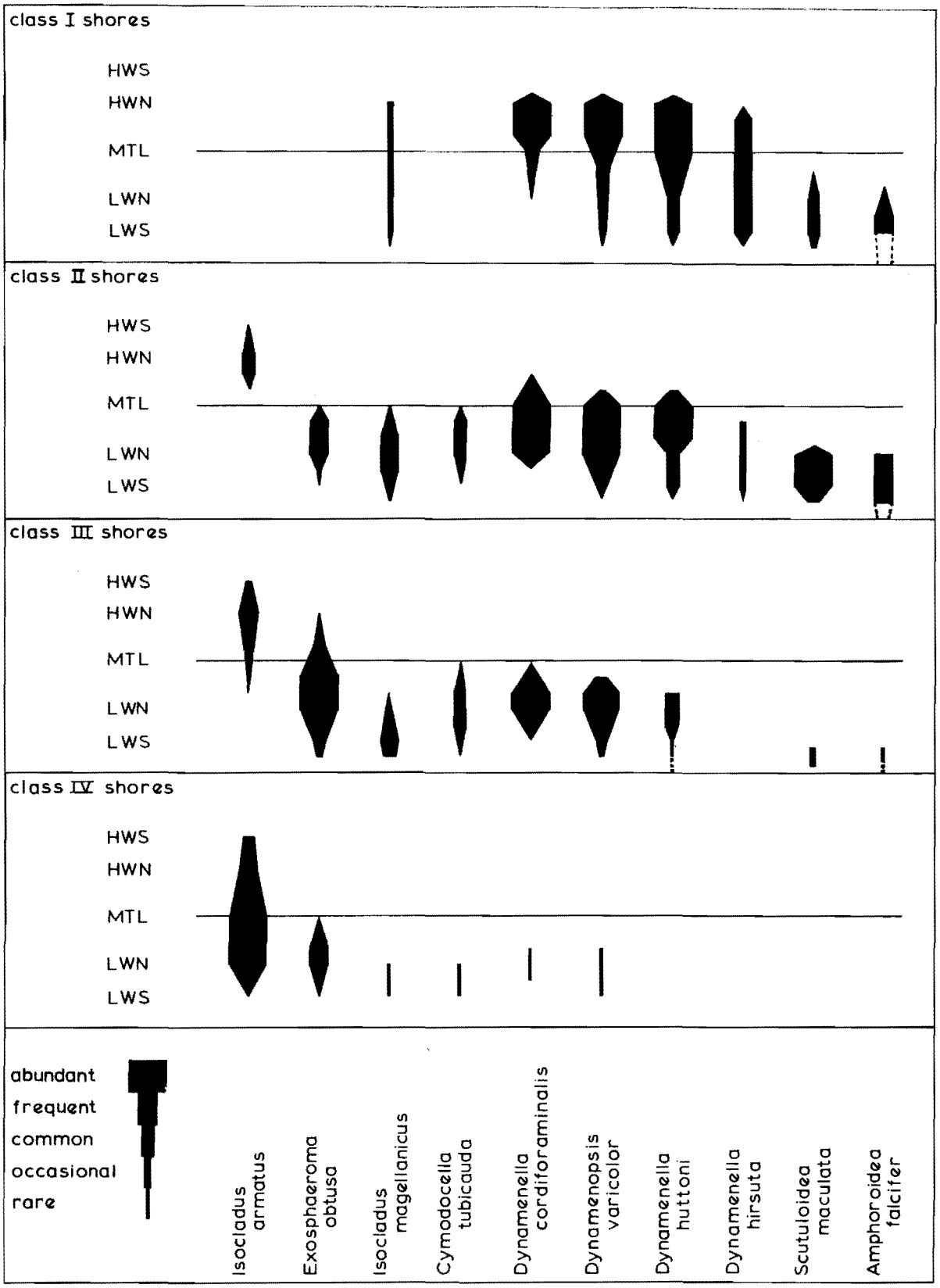

class I shores
HWS
HWN
MTL
LWN
LWS
class II shores
HWS
HWN
MTL
LWN
LWS
class III shores
HWS
HWN
MTL
LWN
LWS
class IV shores
HWS
HWN
MTL
LWN
LWS
abundant
frequent
common
occasional
rare
Isocladus armatus
Exosphaeroma obtusa
Isocladus magellanicus
Cymodocella tubicauda
Dynamenella cordiforaminalis
Dynamenopsis varicolor
Dynamenella huttoni
Dynamenella hirsuta
Scutuloidea maculata
Amphoroidea falcifer

Figure 2

Vertical distribution of 10 intertidal species of Sphaeromidae on the four classes of rocky shore of the Kaikoura Peninsula.

(diameter ca. 10 cm or less) (Plate IX), which are frequently redistributed by the light wave action.

Dominant algae: H. banksii below MTL to LWN
algal turf and Cystophora below LWN

Distribution of rocky shore species

Characteristic assemblages of species occur on each class of rocky shore, vertical zonation and relative abundance of each species varying with wave action (Fig. 2).

Centres of concentration of all species rise with increasing wave action but differences are evident in changes in vertical range. In Isocladus armatus upper limits are constant at HWS but lower limits rise with increasing wave action. In Cymodocella tubicauda and Dynamenella cordiforaminalis both upper and lower limits rise with wave action. In the remaining species lower limits remain constant about LWS but upper limits rise with increasing wave action, except for Exosphaeroma obtusa in which the upper limit at HWN on class III falls to MTL on both class II and class IV (more and less exposed) shores.

Relative abundances also vary with wave action. In I. armatus, E. obtusa, Scutuloidea maculata, and Dynamenella hirsuta, maximum abundance is confined to one shore class, the rapid fall in numbers on other shores indicating

relatively narrow tolerances of wave action or associated conditions. The remaining species are more evenly distributed, but are uniformly rare or absent on class IV shores, indicating low tolerance of conditions associated with reduced wave action.

In the following section, distributions of individual species are examined in relation to wave action and substrate, and variation in distribution of adults and juveniles.

Isocladus armatus

Horizontal distribution

I. armatus are abundant on class IV shores; numbers diminish with increasing exposure to wave action, disappearing on class I shores. On class IV shores, localised concentrations up to about 5000 m^{-2} occur among the mixed stones and sand in and about shallow pools and channels, decreasing as the substrate changes, disappearing on pure rock or sand. On less sheltered shores, where bare rock and larger stones comprise greater, and smaller stones and sand smaller proportions of the substrate, both localised densities and overall relative abundance are lower.

I. armatus are not confined to mixed sand and stones, or to smaller stones on more exposed shores, occurring in small numbers among algae and eelgrass (Zostera sp.), but only adjacent to concentrations on the former substrates.

Vertical distribution

On all except class I shores, I. armatus occur up to HWS; the lower limits however rise from LWS on class IV to above MTL on class II shores; the centres of concentration rise correspondingly from below MTL on class IV to above MTL on class III and about HWN on class II shores.

In I. armatus numbers above HWN fluctuate between successive spring tides: as high tides fall from springs to neaps, the numbers decrease progressively at the higher levels approaching HWS, increasing as high tides rise again to springs. I. armatus alone among the rocky shore species swim freely on incoming tides: at any moment a proportion of the local population is swimming, the remainder resting. A proportion of the swimming individuals rests after being displaced to a higher level, the balance being washed back to a lower level. The individuals left above HWN are exposed to extreme variations in temperature and salinity (Table 10) and to desiccation during neap tides, hence the decrease in numbers, replaced as tides return to springs.

Variation in distribution of adults and juveniles

Samples of I. armatus were taken from MTL, lower mid-littoral, and LWN, on a class IV shore (Wairepo Flat). Juveniles and adults, males and females, were counted at each level and differences evaluated from probabilities based on values of χ^2 (Table 2). Numbers of males and females at

Table 2. Variation in distribution of adults and juveniles in Isocladus armatus on a class IV shore (Wairepo Flat); a. 22 January 1967; b. 11 April 1967.

	adults	juveniles	χ^2	P	males	females	χ^2	P
a.								
MTL	4	228			[0]	[4]		
LML	30	154	65.6	<0.005	19	11	0	1
LWN	10	8			5	3		
b.								
MTL	42	86			21	21		
LML	58	45	67.0	<0.005	34	24	1.0	>0.50
LWN	74	8			39	35		

Note: in this table χ^2 and P refer to both adults and juveniles; numbers of males and females enclosed in brackets were not included in the calculation because of the low values.

each level were not significantly different ($P > 0.50$), but differences between the numbers of adults and juveniles were significant ($P < 0.005$). Although more juveniles occur higher, and more adults lower on the shore, both are present at all levels. The significance of these observations is discussed under 'Breeding Populations'.

Exosphaeroma obtusa

Horizontal distribution

E. obtusa are abundant on class III shores, frequent on class II and IV shores, absent from class I; relative abundance diminishes as wave action increases and decreases from the moderate level. On class III shores concentrations up to 2500 m^{-2} occur under large stones, decreasing in size and number as the substrate changes to rock or smaller stones and sand. E. obtusa occur also on algae, but only in the near vicinity of concentrations among stones.

Vertical distribution

Maximum vertical range, from HWN to LWS, occurs on class III shores; on class II and class IV shores the lower limit remains at about LWS, but the upper limit falls to MTL. Centres of concentration are in the lower mid-littoral on both class II and class III shores, but fall to about LWN on class IV.

Variation in distribution of adults and juveniles

Samples of E. obtusa were taken from MTL and LWN on a class III shore (Whaler's Bay)(Table 3). No adults occurred at MTL; numbers of juveniles were significantly higher ($P < 0.005$) at MTL than at LWN. Smaller individuals appear to be displaced upwards, larger individuals, including breeding adults, being confined to the lower levels.

Isocladus magellanicus

Horizontal distribution

I. magellanicus are frequent on class II and III shores, occasional on class I, rare on class IV shores. Densities reach 200 m^{-2} under stones on class II and III shores; occasional individuals occur also in mixed algal turf on class II, but are confined to holdfasts of Durvillea antarctica on class I shores.

Vertical distribution

Lower limits are about LWS on all shores; upper limits rise with increasing wave action from LWS on class IV to the lower mid-littoral on class III, to MTL on class II, and to HWN on class I shores. Centres of concentration also rise with increasing wave action: LWN to LWS on class III, LWN to lower mid-littoral on class II; on class I shores the small numbers are evenly distributed in the vertical range.

Table 3. Variation in distribution of adults and juveniles in Exosphaeroma obtusa on a class III shore (Whaler's Bay); a. 12 April 1967; b. 7 August 1967.

	adults	juveniles	χ^2	P
a.				
MTL	0	226	42.6	<0.005
LWN	22	107		
b.				
MTL	0	120	20.0	<0.005
LWN	35	60		

Note: in this table χ^2 and P refer only to juveniles.

The small numbers in D. antarctica holdfasts on class I shores were invariably adults, and few juveniles occurred in the algal turf on class II shores, all stages and sizes occurring in consistently larger numbers under stones on class II and III shores.

Variation in distribution of adults and juveniles

Samples of I. magellanicus were taken from above and below LWN on a class III shore (Whaler's Bay) (Table 4). Neither the numbers of males and females nor those of adults and juveniles differed significantly ($P \geq 0.010$) at the two levels.

Cymodocella tubicauda

Horizontal distribution

C. tubicauda are common under stones on class II and III shores, rare on class IV, absent from class I shores. Isolated individuals occur rarely in the shrubby Corallina officinalis and algal turf.

Vertical distribution

Restricted to below LWN on class IV shores, the vertical range extends upwards with increasing exposure to wave action, from LWS to MTL on class III, and from LWN to

Table 4. Variation in distribution of adults and juveniles in Isocladus magellanicus on a class III shore (Whaler's Bay).

	adults	juveniles	χ^2	P	males	females	χ^2	P
Above LWN	11	21			5	6		
Below LWN	38	44	1.4	>0.10	10	28	1.4	>0.10

MTL on class II shores.

Variation in distribution of adults and juveniles

Samples of C. tubicauda were taken from above and below LWN on a class III shore (Whaler's Bay) (Table 5). Numbers of males and females, and of juveniles and adults did not differ significantly at the two levels ($P > 0.10$).

Dynamenella cordiforaminalis

Horizontal distribution

D. cordiforaminalis are abundant on class I, II, and III, rare on class IV shores, occurring almost exclusively in Corallina officinalis, occasionally under stones.

Vertical distribution

Both upper and lower limits rise with increasing wave action, extending from MTL to LWS on class III, from upper mid-littoral to LWN on class II, and from HWN to lower mid-littoral on class I shores. Centres of concentration similarly rise with increasing wave action, from LWN on class III to lower mid-littoral on class II and upper mid-littoral on class I shores, corresponding with zonation in C. officinalis.

Table 5. Variation in distribution of adults and juveniles in Cymodocella tubicauda on a class III shore (Whaler's Bay).

	adults	juveniles	χ^2	P	males	females	χ^2	P
Above LWN	44	24			23	21		
Below LWN	23	6	2.1	>0.10	7	16	2.5	>0.10

Variation in distribution of adults and juveniles

Samples of D. cordiforaminalis were taken from C. officinalis at MTL and LWN on a class II shore (Sugarloaf Rocks) (Table 6). Numbers of adults were low (1 and 5) at MTL compared with LWN (13 and 91); numbers of juveniles were significantly greater ($P < 0.005$), and mean lengths of the samples lower ($P < 0.01$, $P < 0.001$) at the higher level.

Dynamenopsis varicolor

Horizontal distribution

D. varicolor are abundant in Corallina officinalis on class I, II, and III shores, common among crustose corallines and holdfasts of Carpophyllum maschalocarpum on class I and II shores, and under stones on class II and III shores. On class IV shores, D. varicolor are rare, both in C. officinalis and under stones.

Vertical distribution

The lower limit is about LWS on all shores, but the upper limits rise with increasing wave action from LWN on class IV to the lower mid-littoral on class III, to the upper mid-littoral on class II, and to HWN on class I shores.

Table 6. Variation in distribution of sizes, and in adults and juveniles in Dynamenella cordiforaminalis on a class II shore (Sugarloaf Rocks); a. 29 March 1967; b. 9 June 1967.

	N	mean length, mm	SD^2	't'	P
a.					
MTL	158	2.16	0.50	2.75	< 0.01
LWN	191	2.62	0.29		
b.					
MTL	172	2.01	0.55	9.58	<0.001
LWN	109	2.90	0.33		

	adults	juveniles	χ^2	P	males	females
a.						
MTL	1	157	9.0	<0.005	1	
LWN	13	178				13
b.						
MTL	5	167	16.6	<0.005	5	
LWN	18	91			13	5

Variation in distribution of adults and juveniles

Samples of D. varicolor were taken from C. officinalis and from C. maschalocarpum holdfasts etc. on a class II shore (Sugarloaf Rocks) (Table 7). Although both adults and juveniles occurred on all substrates, numbers of adults were significantly smaller ($P < 0.005$) and sample mean lengths lower ($P < 0.001$) in C. officinalis; differences in relative proportions of males and females on the different substrates were not significant ($P > 0.25$, $P > 0.10$).

Dynamenella huttoni

Horizontal distribution

In Corallina officinalis, D. huttoni are abundant on class I and II shores, common on class III and rare on class IV shores. In and among Durvillea antarctica and Carpophyllum maschalocarpum holdfasts, D. huttoni are frequent on class I and common on class II shores; on more sheltered shores where the latter algae are absent, D. huttoni are confined to C. officinalis.

Isolated individuals occur irregularly among other algae such as Cystophora spp. and under stones.

Table 7. Variation in distribution of sizes, and of adults and juveniles in Dynamenopsis varicolor on a class II shore (Sugarloaf Rocks); a. 12 April 1967; b. 21 July 1967.

	N	mean length, mm	SD^2	't'	P
a.					
C. officinalis	95	3.77	3.55	4.97	< 0.001
Holdfasts etc.	22	6.18	2.24		
b.					
C. officinalis	36	5.11	2.80	4.05	< 0.001
Holdfasts etc.	37	7.49	1.42		

	adults	young	χ^2	P	males	females	χ^2	P
a.								
C. officinalis	10	85	35.3	<0.005	5	5	1.0	>0.25
Holdfasts etc.	15	7			8	7		
b.								
C. officinalis	17	19	26.3	<0.005	7	10	1.5	>0.10
Holdfasts etc.	37	0			9	28		

Vertical distribution

From a lower limit about LWS on all shores, the vertical range extends further upward with increasing exposure to wave action, to LWN on class III, to the upper mid-littoral on class II, and to HWN on class I shores. Centres of concentration rise similarly from about LWN on class III to the lower mid-littoral on class II and to the upper mid-littoral on class I shores.

Variation in distribution of adults and juveniles

Samples of D. huttoni were taken from C. officinalis and from D. antarctica and C. maschalocarpum holdfasts on a class I shore (Seal Reef) (Table 8). Numbers of juveniles were significantly greater ($P \leqslant 0.005$) in C. officinalis than in the holdfasts, and sample mean lengths significantly lower ($P \leqslant 0.001$). The total frequencies of all individuals taken in monthly samples are given in Table 9. In the more exposed holdfasts of D. antarctica and C. maschalocarpum, the size frequency distribution was bimodal, larger juveniles and smaller adults appearing in smaller numbers than small juveniles and larger adults. In the less exposed C. officinalis, frequencies of the larger juveniles were again less than those of the smaller, but no adults appeared.

According to Simpson, Roe, and Lewontin (1960, p. 60) bimodality is '. . . usually an indication of faulty

procedure or of heterogeneity of the material included'. The same procedure was applied in sampling all species and in sample analysis, and bimodal frequency distributions did not appear except in D. huttoni. All stages and sizes in D. huttoni are clearly distinguishable morphologically from all other species, and in the absence of sibling species (Mayr 1963, p. 34) the samples were taxonomically homogeneous. While the possibility of sibling species can not be totally excluded, it is desregarded here because of the lack of evidence apart from the size frequency distribution.

Breeding adults are clearly restricted to the more exposed situations in holdfasts of D. antarctica and C. maschalocarpum, a large proportion of newly released young being displaced to the less exposed C. officinalis. If juveniles returned to the more exposed situations to mature and breed, larger proportions of smaller adults would be expected there. Since these do not occur, it appears that juvenile losses are heavy in both situations, the populations being maintained through the high reproductive capacity of the relatively few survivors in the more exposed situations (see also 'Ecological Adaptations' - pp. 71, 93).

Table 8. Variation in distribution of sizes and of adults and juveniles in Dynamenella huttoni on a class I shore (Seal Reef); a. 13 April 1967; b. 4 May 1967.

	N	mean length, mm	SD^2	't'	P
a.					
C. officinalis	115	2.86	4.39	5.69	<0.001
Holdfasts	25	5.04	13.58		
b.					
C. officinalis	45	3.44	2.75	6.92	<0.001
Holdfasts	44	6.70	5.77		

	adults	juveniles	χ^2	P
a.				
C. officinalis	0	115	77.5	<0.005
Holdfasts	10	15		
b.				
C. officinalis	0	45	15.0	<0.005
Holdfasts	28	16		

Note: in this table χ^2 and P refer to juveniles only.

Table 9. *D. huttoni*; distribution of size classes between *Corallina officinalis* and holdfasts of *Durvillea antarctica* and *Carpophyllum maschalocarpum*.

Size classes, mm	2	3	4	5	6	7	8	9	10	11	12	13
C. officinalis	119	199	65	18	5	0	0	0	0	0	0	0
Holdfasts	169	6	4	14	9	11	46	123	58	22	22	7
Totals	288	205	69	32	14	11	46	123	58	22	22	7

Dynamenella hirsuta

D. hirsuta are confined to holdfasts of Durvillea antarctica, and are frequent on class I shores from HWN to LWS, occasional from MTL to LWS on class II shores, absent from class III and IV shores together with D. antarctica.

Scutuloidea maculata

Horizontal distribution

S. maculata are abundant on class II shores, common on class I, occasional on class III, absent from class IV shores, showing a relatively narrow tolerance of wave action.

S. maculata occur mainly on fronds of Carpophyllum maschalocarpum, occasionally on other flat-bladed brown algae such as Glossophora, but only where these are contiguous with large concentrations on C. maschalocarpum.

Vertical distribution

The vertical range is narrow, extending from about LWN to LWS on class I and II shores; on class III shores S. maculata do not occur above LWS, the occasional individuals being irregularly distributed below LWS.

S. maculata are most numerous in the relatively short (ca. 50 cm) dense growths of C. maschalocarpum between LWN and LWS on exposed shores. bove LWN on more exposed and about LWS on more sheltered shores, C. maschalocarpum is sparse and stunted and S. maculata are rare; below LWS, C. maschalocarpum fronds are less dense and more attenuated (several metres in length) and here too S. maculata are rare.

Within the narrow vertical range and variety of substrate, differences in distribution of adults and juveniles were not apparent.

Amphoroidea falcifer

Horizontal distribution

A. falcifer are frequent on class I and II shores, rare on class III and absent from class IV shores. A. falcifer occur almost exclusively on fronds of Carpophyllum maschalocarpum, rarely on other flat-bladed brown algae such as Glossophora and Macrocystis, usually in the vicinity of concentrations on C. maschalocarpum.

Vertical distribution

A. falcifer are rare above LWN on any shore, but extend below LWS, being common on C. maschalocarpum to at least 10 metres depth.

Differences in distribution of adults and juveniles were not apparent.

Discussion

Vertical distribution and relative abundance in each species vary with both wave action (Fig. 2) and substrate (Table 10). Three main categories of substrate appear: a. stones; b. shrubby Corallina officinalis, holdfasts of Durvillea antarctica and Carpophyllum maschalocarpum, crustose corallines, referred to below as 'algal-cryptic'; c. algal fronds, principally of C. maschalocarpum. Each species is predominantly associated with one category of substrate, maximum abundance occurring on a particular class or range of classes of shore, as follows (A = abundant; F = frequent; C = common; O = occasional; R = rare; for numerical values see p. 19):

a. Species living among stones

Shore class	I	II	III	IV
Isocladus armatus		C	F	A
Exosphaeroma obtusa		F	A	F
Isocladus magellanicus	O	F	F	R
Cymodocella tubicauda		C	C	R

On each shore class, the level of greatest concentration is highest in I. armatus, lower in E. obtusa, and lowest in I. magellanicus and C. tubicauda. Thus maximum abundances in I. magellanicus and in C. tubicauda occur at lower levels and on more exposed shores than in E. obtusa

and I. armatus.

b. Algal-cryptic species

Shore class	I	II	III	IV
Dynamenella cordiforaminalis	A	A	A	R
Dynamenopsis varicolor	A	A	A	R
Dynamenella huttoni	A	A	C	
Dynamenella hirsuta	F	O		

Corallina officinalis is distributed more widely both vertically and horizontally than Durvillea antarctica and Carpophyllum maschalocarpum, but with considerable overlap. C. officinalis thus occurs in more sheltered situations as well as on the most exposed rock faces together with the large algae.

Both adults and juveniles of Dynamenella cordiforaminalis occur predominantly among C. officinalis, at higher levels on the more exposed shores. In Dynamenopsis varicolor, juveniles predominate in C. officinalis, adults in the holdfasts of the large algae, but both occur on all the algal-cryptic substrates. In Dynamenella huttoni, only juveniles occur in C. officinalis, both adults and juveniles in the Durvillea and Carpophyllum holdfasts. Both adults and juveniles of Dynamenella hirsuta are confined to Durvillea holdfasts.

Thus among the species in this group, the breeding members of the populations are exposed to progressively

heavier and more prolonged wave action.

c. Algal-frond species

Shore class	I	II	III	IV
Scutuloidea maculata	C	A	R	
Amphoroidea falcifer	F	F	R	

S. maculata is confined to a narrow vertical range between LWN and LWS and is most abundant on class II shores, whereas A. falcifer extends to at least 10 m depth, and is equally numerous on both class I and class II shores. A. falcifer are consequently exposed to a wider range of wave action than S. maculata.

Accordingly, while considerable overlapping occurs among the sympatric species of rocky shores, the habitat-niche of each species is separable, and definable in terms of substrate and wave action, summarised in Table 10.

Table 10. Relative abundance and vertical range of Sphaeromidae on different substrates on four classes of rocky shore (Kaikoura Peninsula); a. class I (very exposed); b. class II (exposed); c. class III (semi-exposed); d. class IV (fairly sheltered) shores.

a.	abundance	range	substrates
I. armatus	absent		
E. obtusa	absent		
I. magellanicus	occasional	HWN - LWS	holdfasts of D. antarctica
C. tubicauda	absent		
D. cordiforaminalis	abundant	HWN - MTL	C. officinalis
	occasional	MTL - LWN	C. officinalis
D. varicolor	abundant	HWN - MTL	C. officinalis
	common	MTL - LWS	among stones in crevices, crustose corallines, holdfasts of C. maschalocarpum
D. huttoni	abundant	HWN - MTL	C. officinalis
	frequent	HWN - LWS	D. antarctica holdfasts
	rare	below LWN	crustose corallines and holdfasts of C. maschalocarpum

Table 10 continued

a.	abundance	range	substrates
D. hirsuta	frequent	HWN - LWS	*D. antarctica* holdfasts
S. maculata	common	LWN - LWS	*C. maschalocarpum* fronds
A. falcifer	frequent	below LWN	*C. maschalocarpum* fronds
b.			
I. armatus	common	HWS - MTL	small stones
E. obtusa	frequent	MTL - LWN	stones
I. magellanicus	frequent	MTL - LWS	stones
C. tubicauda	common	MTL - LWN	stones
D. cordiforaminalis	abundant	MTL - LWN	*C. officinalis*
	rare	about LWN	stones
D. varicolor	abundant	MTL - LWN	*C. officinalis*
	common	LWN - LWS	among stones, crustose coralllines and holdfasts of *C. maschalocarpum*
D. huttoni	abundant	MTL - LWN	*C. officinalis*
	common	MTL - LWS	holdfasts of *D. antarctica* and *C. maschalocarpum*

Table 10 continued

b.	abundance	range	substrates
D. hirsuta	occasional	MTL - LWS	holdfasts of D. antarctica
S. maculata	abundant	LWN - LWS	C. maschalocarpum fronds
A. falcifer	frequent	below LWS	C. maschalocarpum fronds
c.			
I. armatus	frequent	HWS - MTL	small stones
	occasional	MTL - LWN	medium stones
E. obtusa	occasional	HWN - MTL	small stones
	abundant	MTL - LWN	large stones
	frequent	LWN - LWS	large stones
	occasional	LWN - LWS	large stones
I. magellanicus	frequent	LWN - LWS	large stones
C. tubicauda	common	below MTL	large stones
D. cordiforaminalis	abundant	about LWN	C. officinalis
	occasional	about LWN	stones
D. varicolor	abundant	about LWN	C. officinalis
	common	below LWN	stones
D. huttoni	common	about LWN	C. officinalis
	rare	below LWN	Cystophora
D. hirsuta	absent		
S. maculata	rare	below LWS	various algae
A. falcifer	rare	below LWS	various algae

Table 10 continued

d.	abundance	range	substrates
I. armatus	common	HWS - MTL	mixed small stones and sand
	abundant	MTL - LWN	mixed small stones and sand
	occasional	below LWN	mixed small stones and sand
	common in algal drift floating at low tide		
E. obtusa	frequent	about LWN	mixed stones and sand
I. magellanicus	rare	below LWN	stones, algal turf
C. tubicauda	rare	below LWN	stones, algal turf
D. cordiforaminalis	rare	below LWN	stones, algal turf
D. varicolor	rare	below LWN	stones, algal turf
D. huttoni	absent		
D. hirsuta	absent		
S. maculata	absent		
A. falcifer	absent		

Brackish water species

Sphaeroma quoyana, Paradynamenopsis crenellata, and Pseudosphaeroma campbellensis were collected in or near fresh water at Hatfields Beach, in the Heathcote-Avon Estuary, and at Portobello (Otago Harbour) respectively (Fig. 1). Each locality is more sheltered from wave action than any of the rocky shores of the Kaikoura Peninsula. Sphaeroma quoyana and Pseudosphaeroma campbellensis have been recorded from localities in which the influence of fresh water may be small (see Hurley 1961); Paradynamenopsis crenellata has not been previously recorded. These species therefore may not be confined to brackish waters. They may however be designated 'brackish water species' to distinguish them from strictly marine species, since Isocladus armatus and Exosphaeroma obtusa also occur at Hatfields Beach and Portobello, but not in the near vicinity of the fresh water.

Sphaeroma quoyana

On Hatfields Beach, a tidal creek flows through sand and soft sandstone on to a gently sloping and sheltered beach. S. quoyana is frequent in burrows in the sandstone (often several in a burrow), in the upper midlittoral zone, above the surface of the fresh water.

Paradynamenopsis crenellata

Clusters of small Mytilus are attached to wooden structures extending from the shore in the Heathcote-Avon Estuary. P. crenellata are abundant among the clusters from about HWN to MTL, being thus drained and exposed to the air on each low tide. Smaller numbers occur at and below MTL, in shallow pools among green algae (chiefly Ulva lactuca), and in crevices (not burrows) in the wooden structures.

Pseudosphaeroma campbellensis

At Portobello, a small stream flows out over a very flat and sheltered shore comprising silty sand and stones. P. campbellensis are frequent in and about the fresh water flow, under stones at about MTL.

ECOLOGICAL ADAPTATIONS

Horizontal and vertical distribution of rocky shore sphaeromid species are closely related to both substrate and wave action. In a number of species, significant proportions of juveniles were found at higher levels and on different substrates from the adults, greater separation of juveniles and adults occurring in the more exposed algal-cryptic species. The brackish water species may not be restricted to this habitat, but are distinguished from the strictly marine species which do not occur in the near vicinity of fresh water.

In this section, external morphology, tolerances of temperature, salinity, and desiccation in rocky shore and brackish water species, and breeding populations of rocky shore species, are examined, to compare the ecological adaptations of the species, and the effects of the environmental factors.

1. External morphology

A number of authors (see Dahl 1948; Wieser 1959) have examined the relationship between morphology and ecology. Variation among sphaeromid species in the form of the body and of the appendages, especially pereopods and mandibles appear to be related to both wave action and substrate.

a. Species living among stones

In Isocladus armatus (Fig. 3), Exosphaeroma obtusa (Fig. 6), and Isocladus magellanicus (Fig. 7), the body is moderately flattened, and otherwise similar except that males of E. obtusa lack the spine on the seventh pereonal tergite, characteristic of Isocladus males. Cymodocella tubicauda (Fig. 8) are deep dorso-ventrally, considerably smaller than the other species, and shelter in small surface irregularities, too shallow to accommodate the larger species.

The body is heavier in I. magellanicus and C. tubicauda, characteristic of more exposed shores, than in I. armatus and E. obtusa, of less exposed shores. In the four species, thick pads of short setae covering the median surfaces of the pereopods help to grip the surfaces of smooth stones. In I. magellanicus and C. tubicauda, strong serrated spines protruding at intervals from the pads help the claws to grip the rough encrusting coralline algae which are common on the more exposed shores.

The mandibles are similar in I. armatus, E. obtusa and I. magellanicus. The molar processes are coarsely serrated, the laciniae mobiles well developed, and the incisor processes moderately sclerotised and with distinct teeth. In C. tubicauda, the molar processes and laciniae mobiles are again similar, but the teeth of the incisor processes are fused into unbroken gouge-shaped cutting edges.

Examination of gut contents showed that calcareous

material (identified by solution in hydrochloric acid) was a major constituent in the diet of C. tubicauda, evidently derived from the calcareous prostrate coralline algae covering the stones among which the species is most common. In I. armatus, E. obtusa, and I. magellanicus, calcareous material was not detected; gut contents consisted of sand, algal cells and sporelings, and minute crustacean appendages, usually of the locally abundant sphaeromid species. Cannibalisation of moulting or dead or moribund individuals in these species was observed in the laboratory, together with acceptance of a range of shellfish meat (gastropods, bivalves, chitons).

b. Algal-cryptic species

In Dynamenella cordiforaminalis (Fig. 9), Dynamenopsis varicolor (Fig. 10), and Dynamenella huttoni (Fig. 11), the body is strongly constructed, the pereopods stout, with well developed setal pads with strong spines protruding at intervals, and with large strong and heavily sclerotised claws. These three species are commonly exposed to direct wave action, the strength of the exoskeleton reducing the susceptibility to mechanical damage. In Dynamenella hirsuta (Fig. 12), which occur only beneath the holdfasts of Durvillea antarctica, fully protected from direct wave action, the body is rather light and fragile, although the pereopods are again strong with well developed spines and claws.

In Dynamenella cordiforaminalis, D. huttoni, and D. hirsuta, the mandibles resemble those of Isocladus armatus, but in Dynamenopsis they are more like those of Cymodocella tubicauda, but heavier, the teeth being fused into very blunt and heavily sclerotised edges. Gut contents in Dynamenopsis varicolor again contained a large proportion of calcareous material, as in C. tubicauda; in the three remaining species, gut contents comprised varying proportions of sand, algal sporelings and unidentified algal material. This was predominantly brown in Dynamenella huttoni and D. hirsuta, being derived from the holdfasts of Durvillea and Carpophyllum.

c. Algal-frond species

Both Scutuloidea maculata (Fig. 13) and Amphoroidea falcifer (Fig. 14) occur predominantly on the fronds of Carpophyllum maschalocarpum at and below LWN on more exposed shores. The floating fronds absorb most of the wave shock, so that the main requirement is to avoid displacement by the direct effect of wave action or by the fronds rubbing together.

In both species the body is flattened dorso-ventrally, and is relatively light and fragile. In both species the first pereopods are short, the second, third, and seventh very long. In S. maculata, the fourth, fifth, and sixth pereopods are also long, with small claws; the median adhesive pads of setae are absent, short stout spines protruding at intervals from the inner surfaces. In A. falcifer, the fourth, fifth, and sixth pereopods are relatively short

and extremely stout with very large and strong claws.

The mandibles in both S. maculata and A. falcifer resemble those in Isocladus armatus (Fig. 3), but the incisor processes are shallower dorso-ventrally, and the tips of the teeth are more broadly rounded, perhaps related to a diet consisting exclusively of live algae, epiphytes and spore-lings and the algal substrate.

d. Brackish water species

The brackish water habitats are uniformly sheltered from wave action, and the bodies of the brackish water species are relatively light and fragile, the pereopods being slender with small claws. In Pseudosphaeroma campbellensis (Fig. 16), living under stones, the body is flattened dorso-ventrally. In Sphaeroma quoyana (Fig. 15), living in burrows, and Paradynamenopsis crenellata (Fig. 17), living among clusters of Mytilus, the body section is deep, resembling that of the algal-cryptic species.

Field observations were not made, but all three brackish water species swim freely in the laboratory. In Sphaeroma quoyana, the largest of the three species, and with the deepest body section, long ('swimming') setae fringe the outer surfaces of the first three pairs of pereopods, the last four pairs being broad and flattened with dense short setae forming fringes on both inner and outer margins. The long setae and the flattening of the pereopods are evidently a means of

extending the surface area, compensating for the loss in buoyancy from the deep body section, and facilitating swimming.

In Pseudosphaeroma campbellensis, living under stones, the pereopods resemble those of the rocky shore species living among stones, being slender with small claws. In Paradynamenopsis crenellata on the other hand, living among clusters of Mytilus, the pereopods are more slender than, but otherwise resemble those of the algal-cryptic species.

The mandibles of Sphaeroma quoyana are similar to those of Cymodocella tubicauda and Dynamenopsis varicolor, but are clearly adaptive to the boring habit, although S. quoyana occur also in mudflats and are thus not restricted to boring in wood or stone (Hurley 1961). The mandibles in both Pseudosphaeroma campbellensis and Paradynamenopsis crenellata are similar, and resemble those of the pattern common in the rocky shore species, for example Isocladus armatus (Fig. 3).

Discussion

Some morphological trends appear to correspond with differences in the shore habitats. The body is heavier in the species typically exposed to heavier wave action. Apparent exceptions in the algal-cryptic and algal-frond species, Dynamenella hirsuta, Scutuloidea maculata, Amphoroidea falcifer, live in situations on exposed shores in which they are completely or partly protected from wave

action. In the species of more sheltered shores, including those of brackish waters, the pereopods are relatively uniform, slender, and with small claws. In the algal-cryptic species, characteristic of exposed shores, the pereopods are again uniform, but stout and with large and strong claws. In the algal-frond species, further variations occur. In Amphoroidea falcifer, the second, third, and seventh pereopods are slender and elongated and with small claws; the fourth, fifth, and sixth pereopods are very stout and with very large claws, resembling those of fish-lice of the families Aegidae and Cymothoidae (Isopoda). In Scutuloidea maculata, all but the first pereopods are slender and elongated, and with small claws. As described above (see 'Ecological Distribution'), S. maculata is most abundant in the dense foliose low-intertidal growth of Carpophyllum maschalocarpum, whereas A. falcifer is more evenly distributed among the low-intertidal growth and the sparser and more elongated sublittoral growth. The leaflets of the foliose growth are small enough for S. maculata to grip the margins by opposing the distal articles and claws to the elongated penultimate articles of the pereopods, impossible on the wider, thicker fronds. Thus in S. maculata the grip is strengthened by increasing the leverage by elongating the legs. A. falcifer on the other hand, grip the broader fronds more firmly by means of the powerful claws, the leverage being strengthened by increasing the cross-sectional

area of the legs and internal muscles.

Other differences appear in the morphology of the pereopods. In all species except Scutuloidea maculata, the inner surfaces of either two or three of the penultimate articles are covered with dense pads of fine setae. In all the algal-inhabiting species, in Paradynamenopsis crenellata (brackish water), and Isocladus magellanicus and Cymodocella tubicauda (among stones on exposed shores), serrated spines protrude at intervals from the setal pads.

According to Naylor (1955d) "The second pair of legs of males of all species [of Idotea] bear thick pads of fine setae on their inner surfaces. This pair of legs is used by the male in clasping the female in the periods of pairing prior to copulation, when it would appear that the pads of setae give a good grip on the smooth surface of the female." Where they occur in the sphaeromid species studied, the setal pads are present in both males and females and in juveniles. The pads are absent in Scutuloidea maculata, and reduced in Amphoroidea falcifer; in these species, the male clasps the female with the third to sixth legs, the elongated second and seventh grasping the algal frond. It appears that in sphaeromids, the primary function of the pads of setae is to reinforce the grip on the substrate, although they also serve in pairing, as in Idotea. In the species living among stones on more exposed shores (Isocladus magellanicus, Cymodocella tubicauda), and in all those living

among algae, the grip appears to be further reinforced by the spines protruding from the setal pads.

In general, the mouthparts appear to be functionally similar, but some obviously adaptive differences occur in the incisor processes of the mandibles. In the majority of species the incisor processes vary only slightly from a broadly adaptive pattern consisting of moderately sclerotised and distinct teeth. In Cymodocella tubicauda, Dynamenopsis varicolor, and Sphaeroma quoyana, the teeth are fused into solid gouge-shaped structures, adaptive to dietary differences in the two former species, and to the boring habit in the latter.

Other morphological differences are harder to evaluate ecologically. Sculptured and tubercular or granulated body surfaces are characteristic of several species, and might appear to be a means of strengthening the exoskeleton. This ornamentation is however invariably more prominent in males than in females, and in adults than in juveniles, in the species studied. The adaptive value, if any, remains obscure, but is not obviously related directly to wave action.

Hansen (1905) suggested that males and females in some species of Sphaeromidae may differ ecologically, because of sexual differences in morphology, particularly of the telson. No such ecological differences were found in any of the species included in the present study, although differences

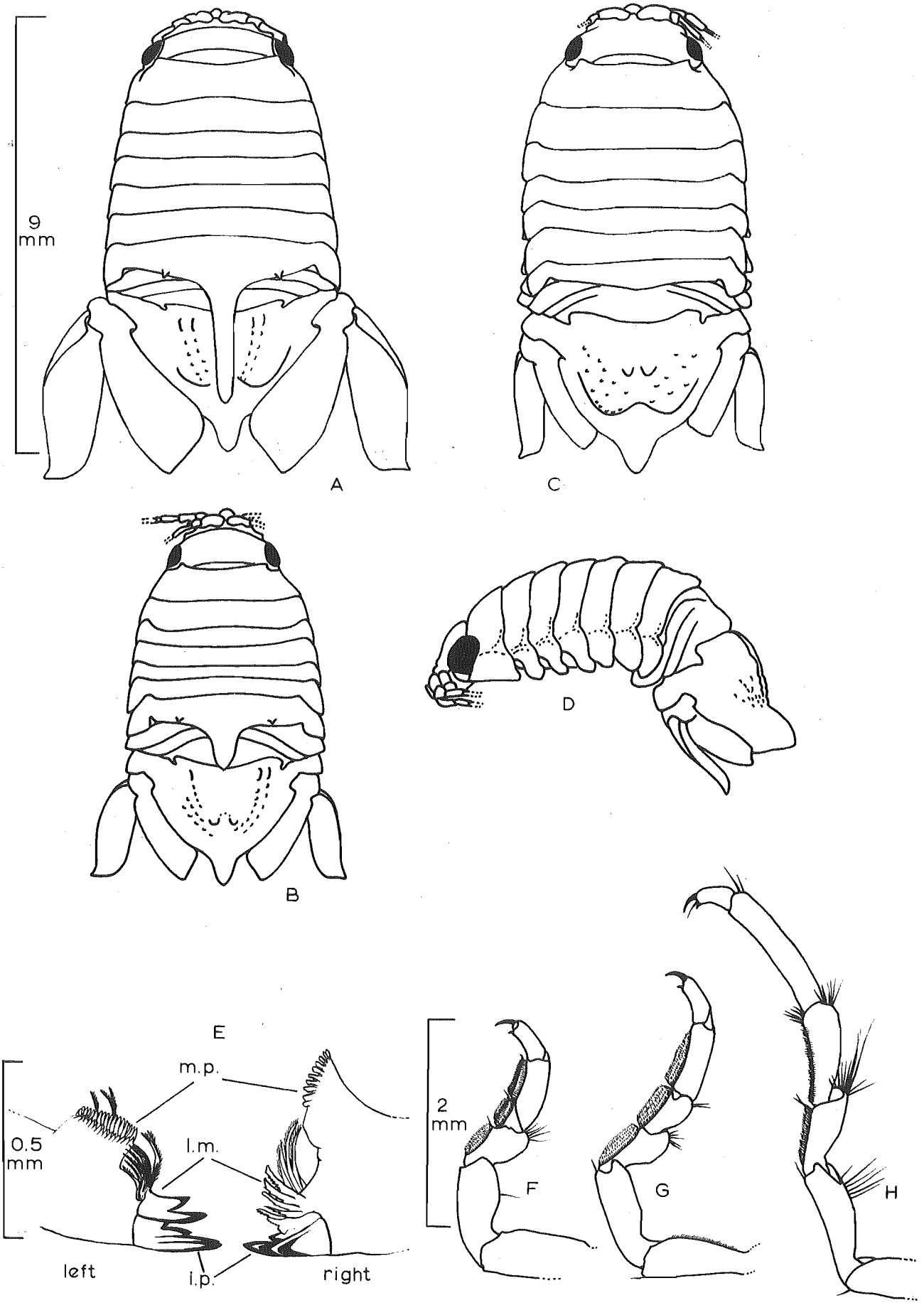
in distribution of adults and juveniles occur in several species (see 'Ecological Distribution').

Variations in colour, or in patterns of pigmentation, or in both, occur in the majority of species studied. Colours vary in Cymodocella tubicauda, Dynamenella cordiforaminalis and D. huttoni, and Dynamenopsis varicolor, independently of age, sex, or substrate. Both colours and patterns vary in Isocladus armatus and I. magellanicus, Exosphaeroma obtusa, Scutuloidea maculata, Amphoroidea falcifer, and Pseudosphaeroma campbellensis, again apparently independently of age, sex, or substrate. Coloration is always cryptic, blending with the colours of the substrates on which each species occurs predominantly. The adaptive significance of the variation in coloration is thus not always clear. Colour variation in Sphaeroma serratum in France (Bocquet, Lévi, and Teissier, 1951), and in S. rugicauda in Britain (West, 1964), was found to be genetically controlled, relative frequencies of different colour morphs varying geographically and seasonally. In Isocladus armatus, in New Zealand, colour variation was found to be related to differences in tolerance of temperature and salinity (see 'Phenotypic Variation in Isocladus armatus'). Colour variation in these species thus appears to be associated with physiological differences rather than directly adaptive; whether the same condition exists in other sphaeromid species would need further investigation.

The ecological significance of differences in the form of the pleopods (see 'Introduction - External Morphology') also remains obscure. Except for the hemibranchiate Isocladus magellanicus, all the species of the exposed rocky shores studied are eubranchiate; except for the eubranchiate Paradynamenopsis crenellata, all the species of sheltered shores (including brackish water) are hemibranchiate. No platybranchiate species were included in this study, but Cassidina typa is a common and widespread sublittoral species (trawled at Kaikoura from about 20 fm. on shelly bottoms; see also Hurley, 1961); Paravireia typica on the other hand appears to be a brackish or freshwater form (Hurley, 1961). Thus the form of the pleopods does not appear to restrict the capacity of the species with respect to physiological adaptation (see also 'Tolerance of Temperature, Salinity, and Desiccation').

Species in which the body is less robust and in which the pereopods are less strongly developed will be subject to damage and displacement by wave action, and therefore less successful on more exposed shores. Conversely, the success of species adapted to clinging to and sheltering among algae may be less because of the reduced extent and variety of suitable substrates on less exposed shores. There seems to be little doubt therefore that interaction between external

morphology and the conditions of wave action and substrate is at least partly responsible for the differences in distribution and abundance of the sphaeromid species.


9
mm
A
C
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D
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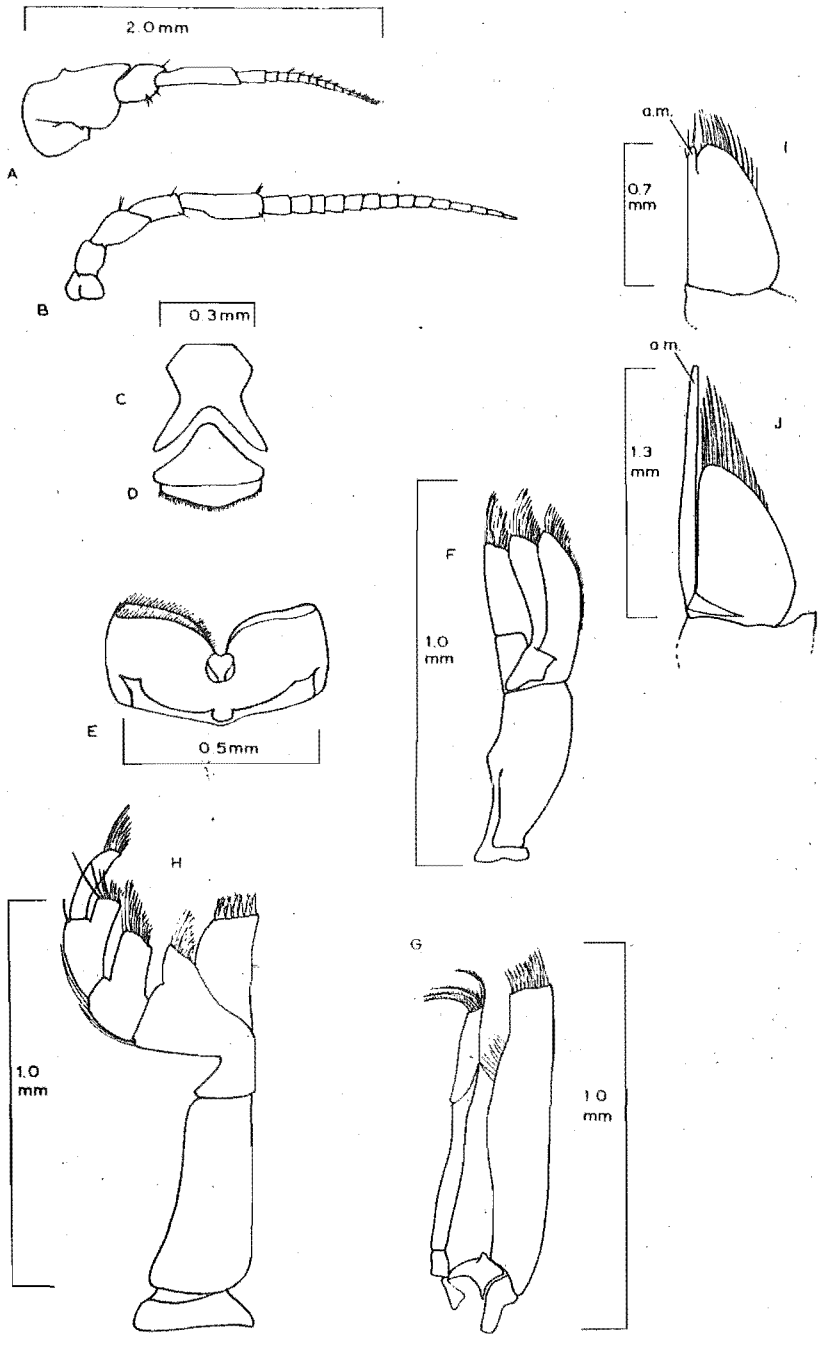
m.p.
l.m.
0.5
mm
left
l.p.
right
2
mm
F
G
H

Fig. 3

Isocladus armatus

A, mature male; B, immature male; C, D, dorsal and lateral aspects of female (thoracic legs omitted); E, mandibles; m.p., molar processes; l.m., laciniae mobiles; i.p., incisor processes; F, G, H, first, fourth and seventh thoracic legs.


2.0mm
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C
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F
1.0
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a.m.
I
0.7
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a.m.
J
1.3
mm
H
1.0
mm
G
1.0
mm

Fig. 4.

Isocladus armatus: A, antenna I; B, antenna II; C, epistome; D, labrum; E, paragnath; F, maxilla I; G, maxilla II; H, maxilliped; I, inner ramus of pleopod 2 showing rudimentary appendix masculina (a.m.), immature male; J, inner ramus of pleopod 2 showing fully developed appendix masculina in mature male.

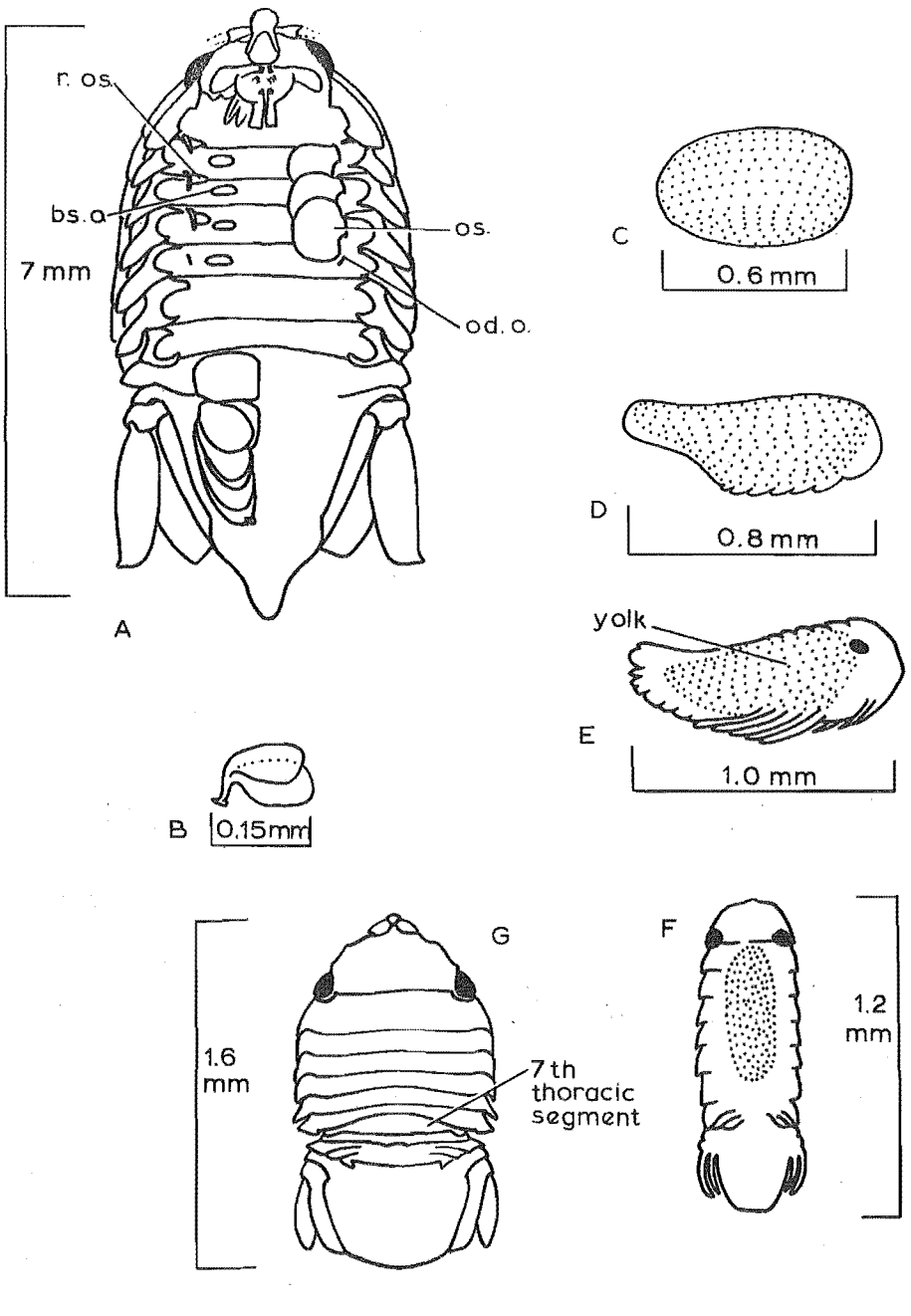
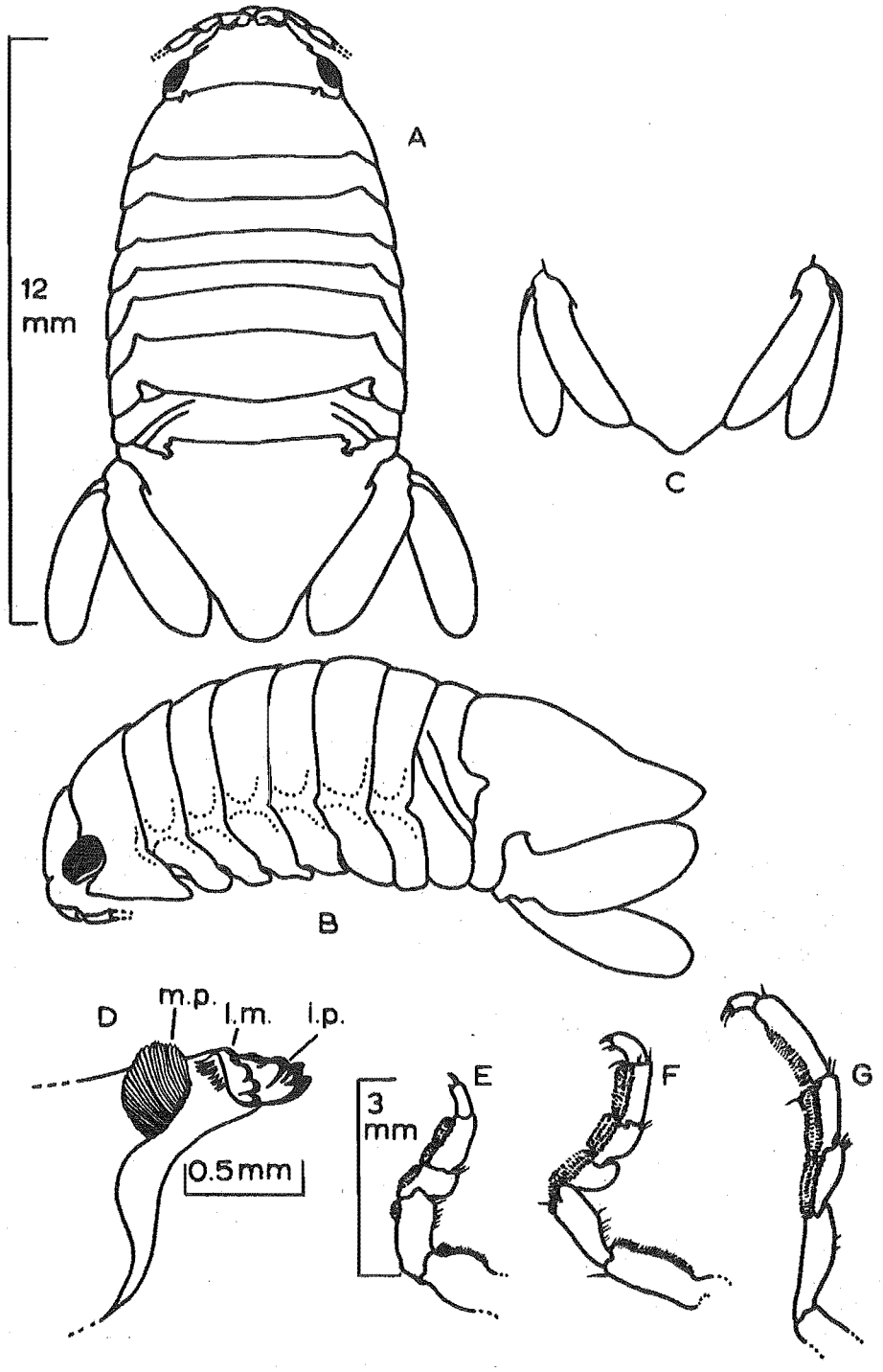

r. os.
bs.o.
os.
od. o.
7 mm
A
C
0.6 mm
D
0.8 mm
yolk
E
1.0 mm
B
0.15mm
G
1.6 mm
7 th thoracic segment
F
1.2 mm

Fig. 5

Isocladus armatus: A, ventral view of female showing rudimentary oostegites (r. os.), rudimentary brood sacs and openings (bs. o.), fully developed oostegites (o s.), and position of oviducal opening (od.o.); B, rudimentary brood sac; C to G, stages in embryonic development.


12
mm
A
C
B
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m.p.
l.m.
l.p.
0.5mm
3
mm
E
F
G

Fig. 6

Exosphaeroma obtusa

A, B, dorsal and lateral aspects of male;
C, dorsal aspect of female telson; D, left mandible;
E, F, G, first, fourth, and seventh thoracic legs.

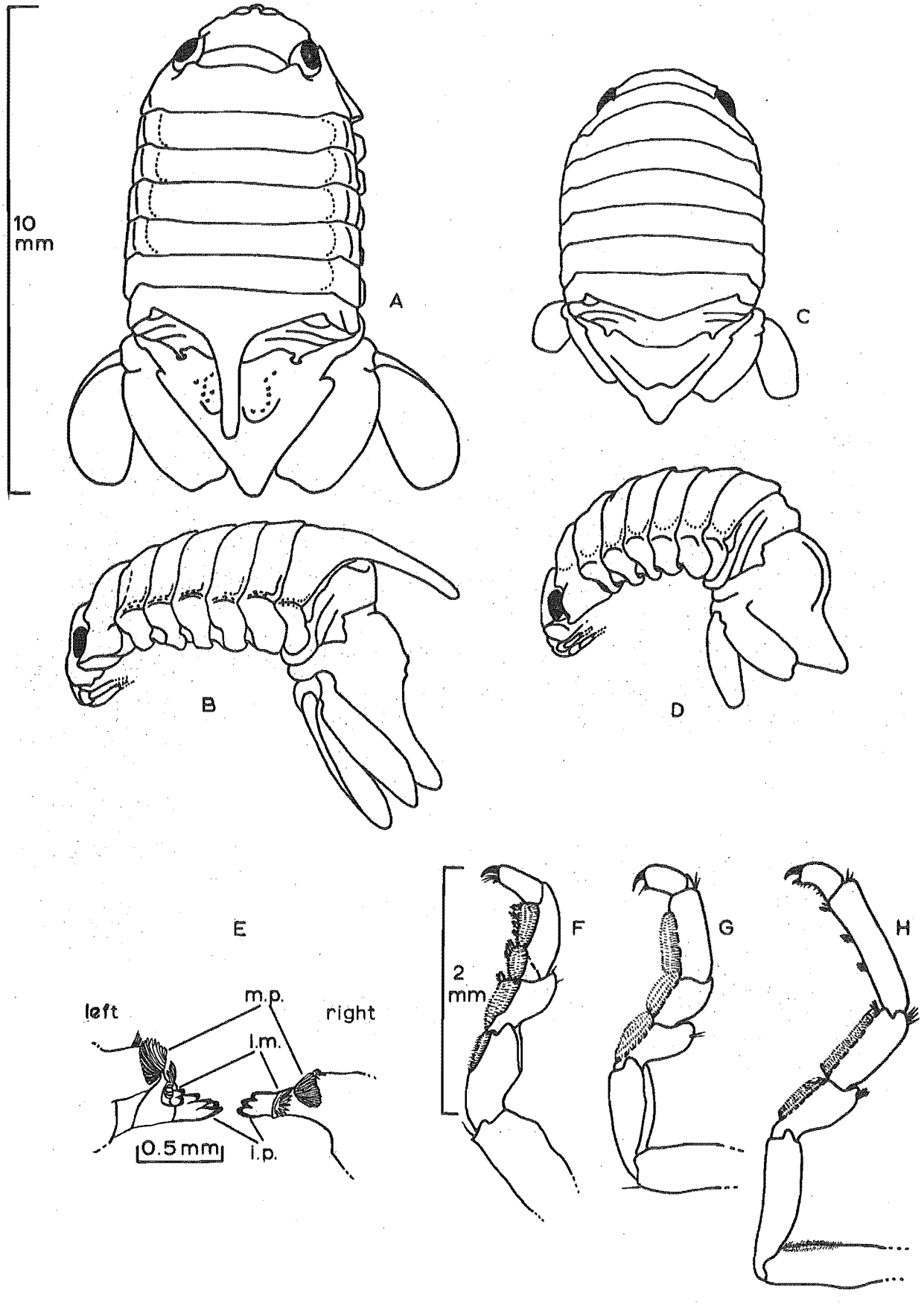
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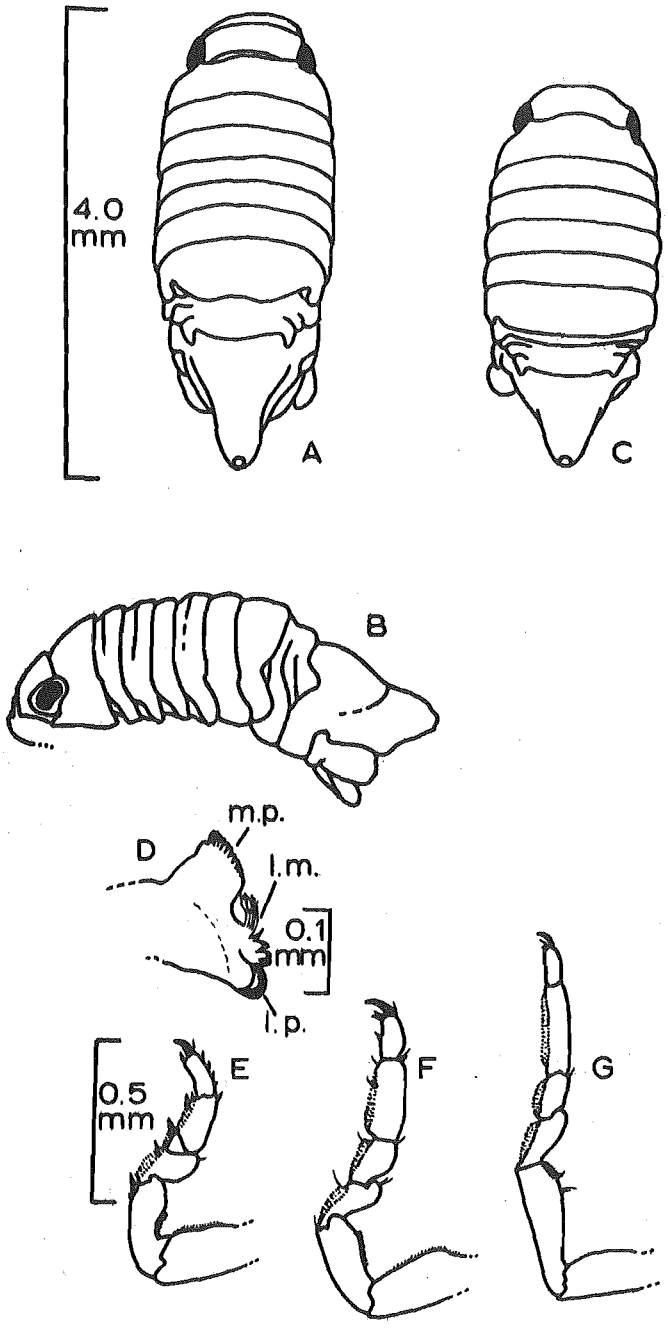
Fig. 7

Isocladus magellanicus

A, B, dorsal and lateral aspects of mature male; C, D, dorsal and lateral aspects of female; E, mandibles; F, G, H, first, fourth, and seventh thoracic legs.


4.0
mm
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C
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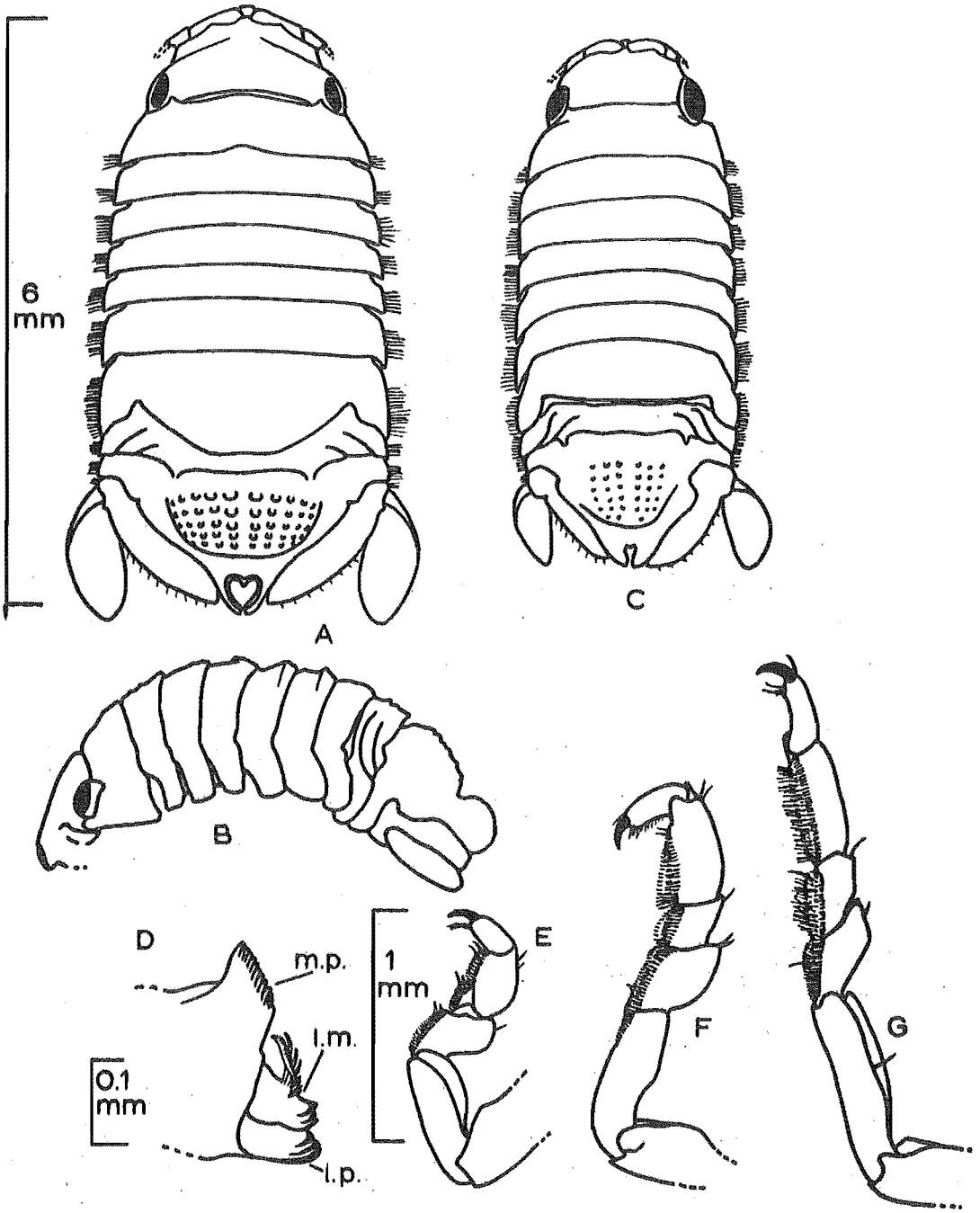
m.p.
D
l.m.
0.1
mm
l.p.
0.5
mm
E
F
G

Fig. 8

Cymodocella tubicauda

A, B, dorsal and lateral aspects of male; C, female; D, left mandible; E, F, G, first, fourth, and seventh thoracic legs.


6
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0.1
mm
l.p.
1
mm
E
F
G

Fig. 9

Dynamenella cordiforaminalis

A, B, dorsal and lateral aspects of male; C, female; D, left mandible; E, F, G, first, fourth, and seventh thoracic legs.

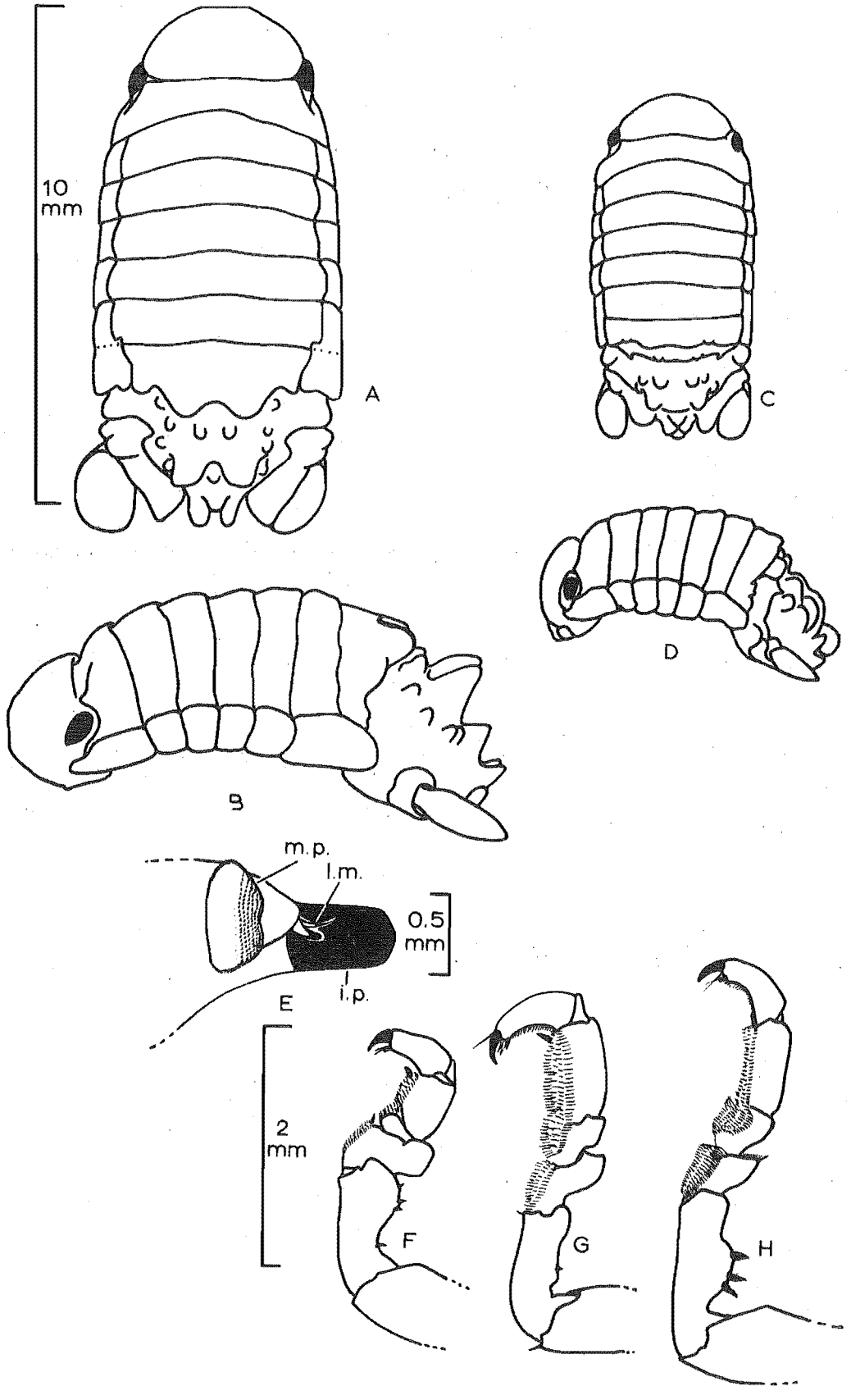
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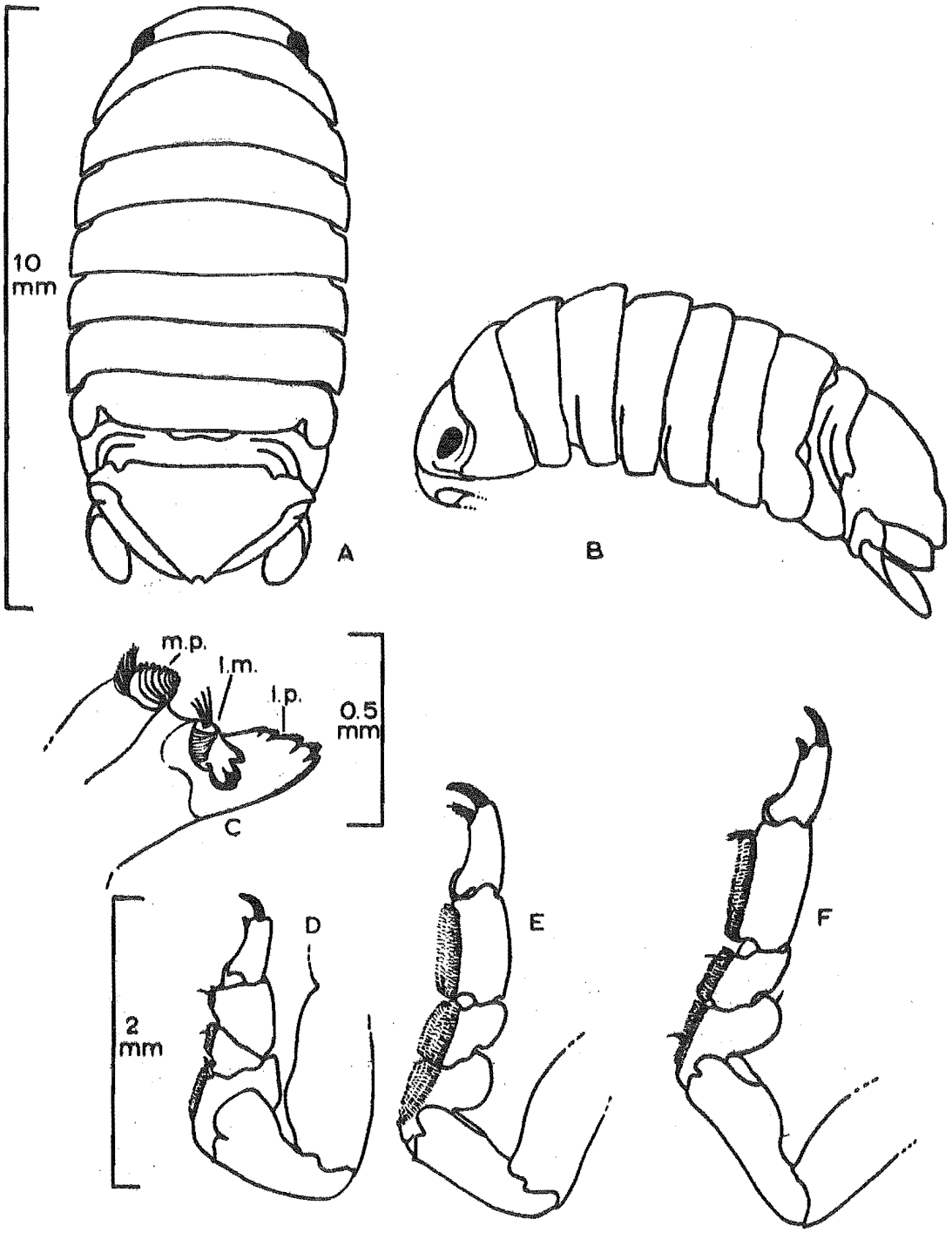
Fig. 10

Dynamenopsis varicolor

A, B, dorsal and lateral aspects of male; C, D, dorsal and lateral aspects of female; E, left mandible; F, G, H, first, fourth, and seventh thoracic legs.


10
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0.5
mm
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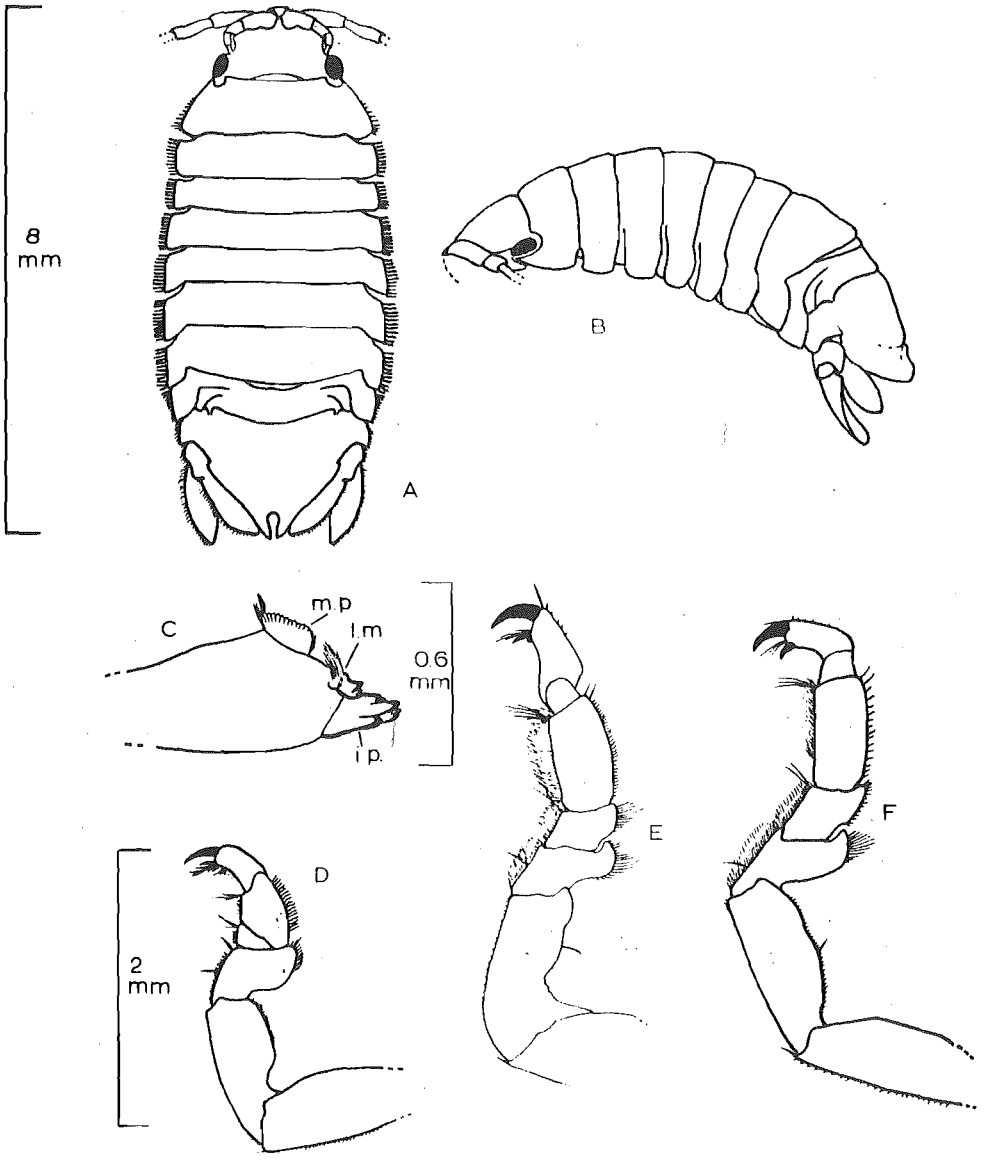
mm
D
E
F

Fig. 11

Dynamenella huttoni

A, B, dorsal and lateral aspects of male; C, left mandible; D, E, F, first, fourth, and seventh thoracic legs.


8
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A
B
C
m.p
l.m
l.p.
0.6
mm
D
2
mm
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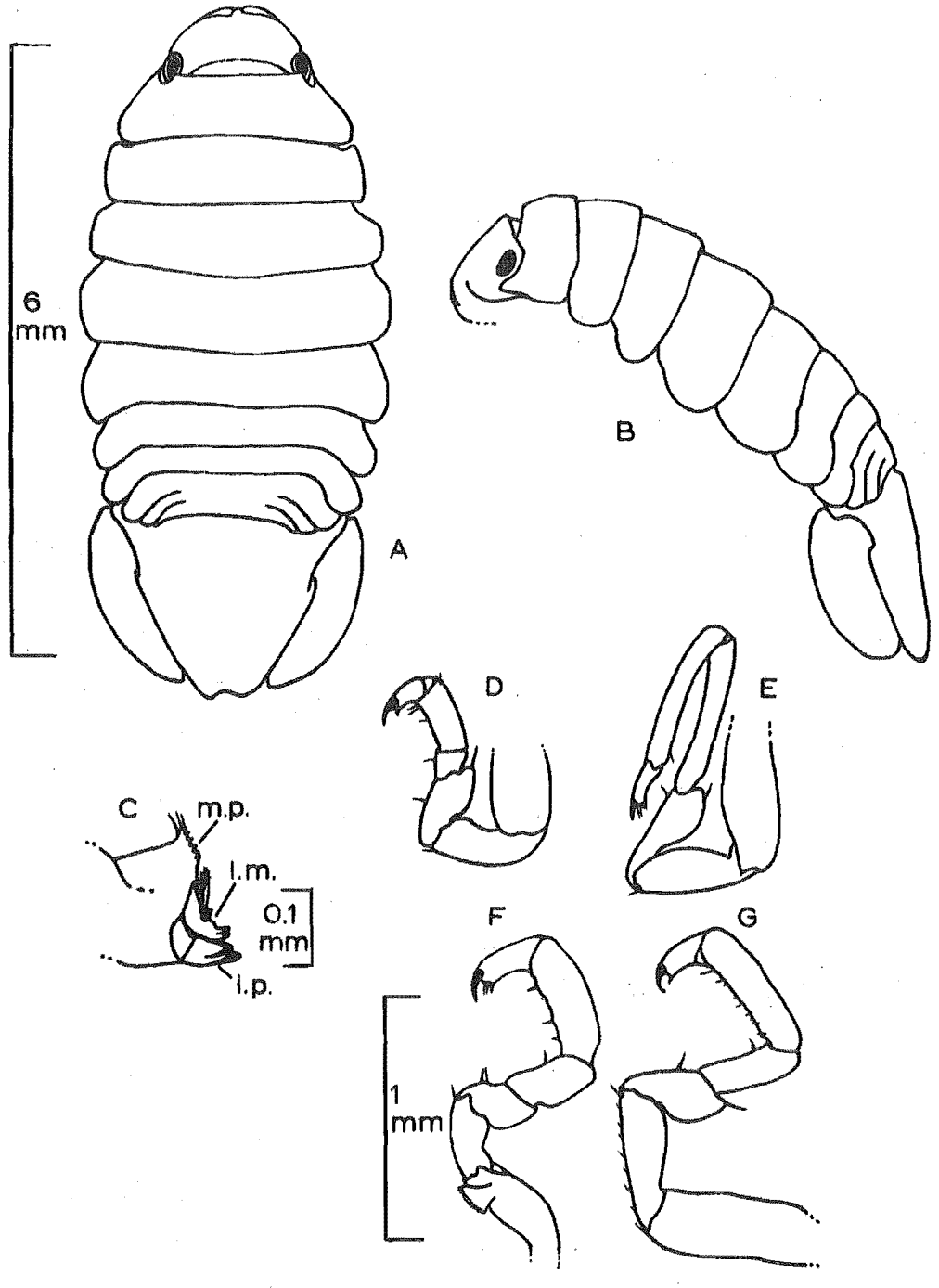
F

Fig. 12

Dynamenella hirsuta

A, B, dorsal and lateral aspects of male; C, left mandible; D, E, F, first, fourth, and seventh thoracic legs.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1
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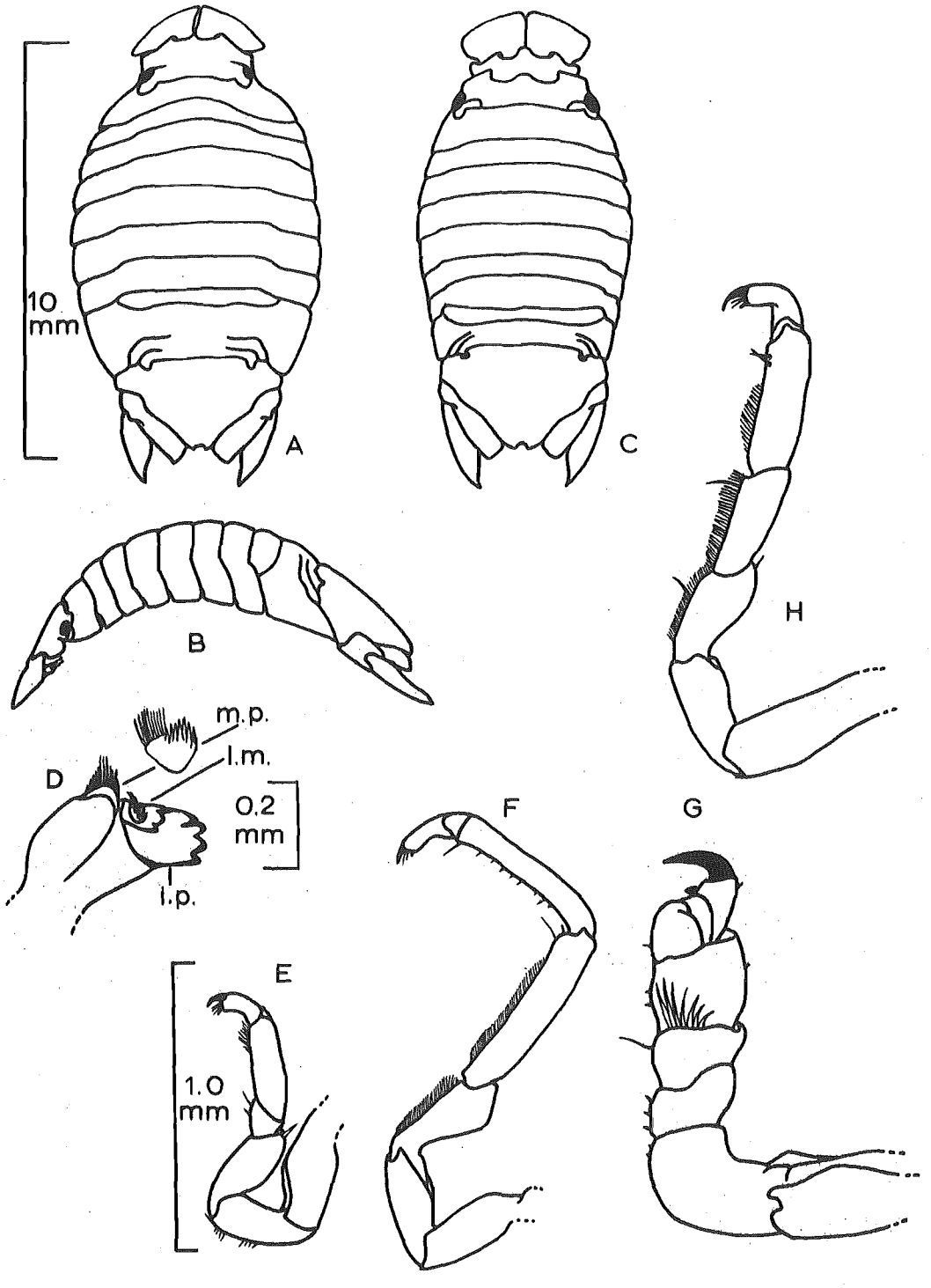
Fig. 13

Scutuloidea maculata

A, B, dorsal and lateral aspects of male; C, left mandible; D, E, F, G, first, second, fourth and seventh thoracic legs.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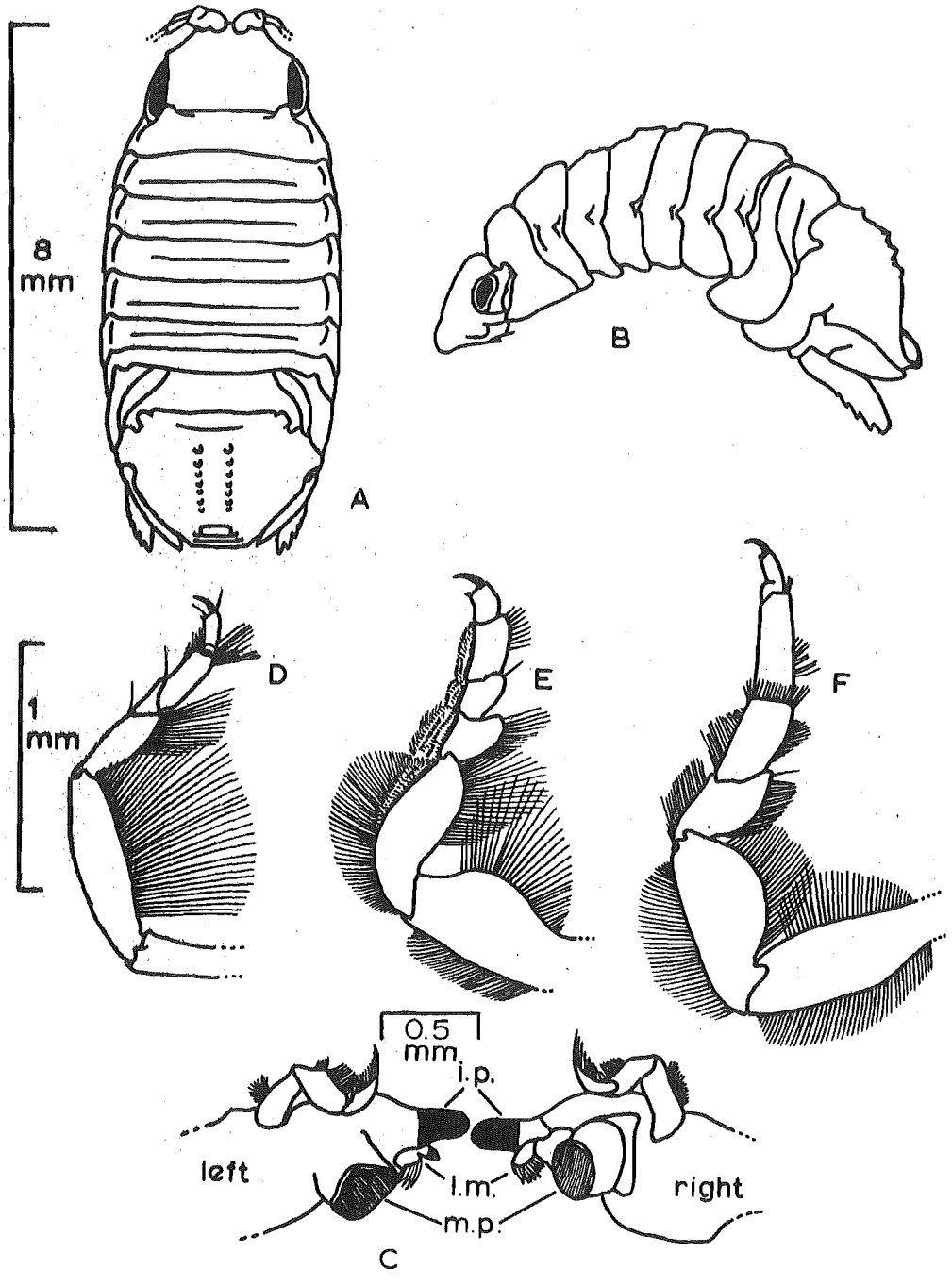
mm

Fig. 14

Amphoroidea falcifer

A, B, dorsal and lateral aspects of male; C, female; D, left mandible; E, F, G, H, first, second, fourth, and seventh thoracic legs.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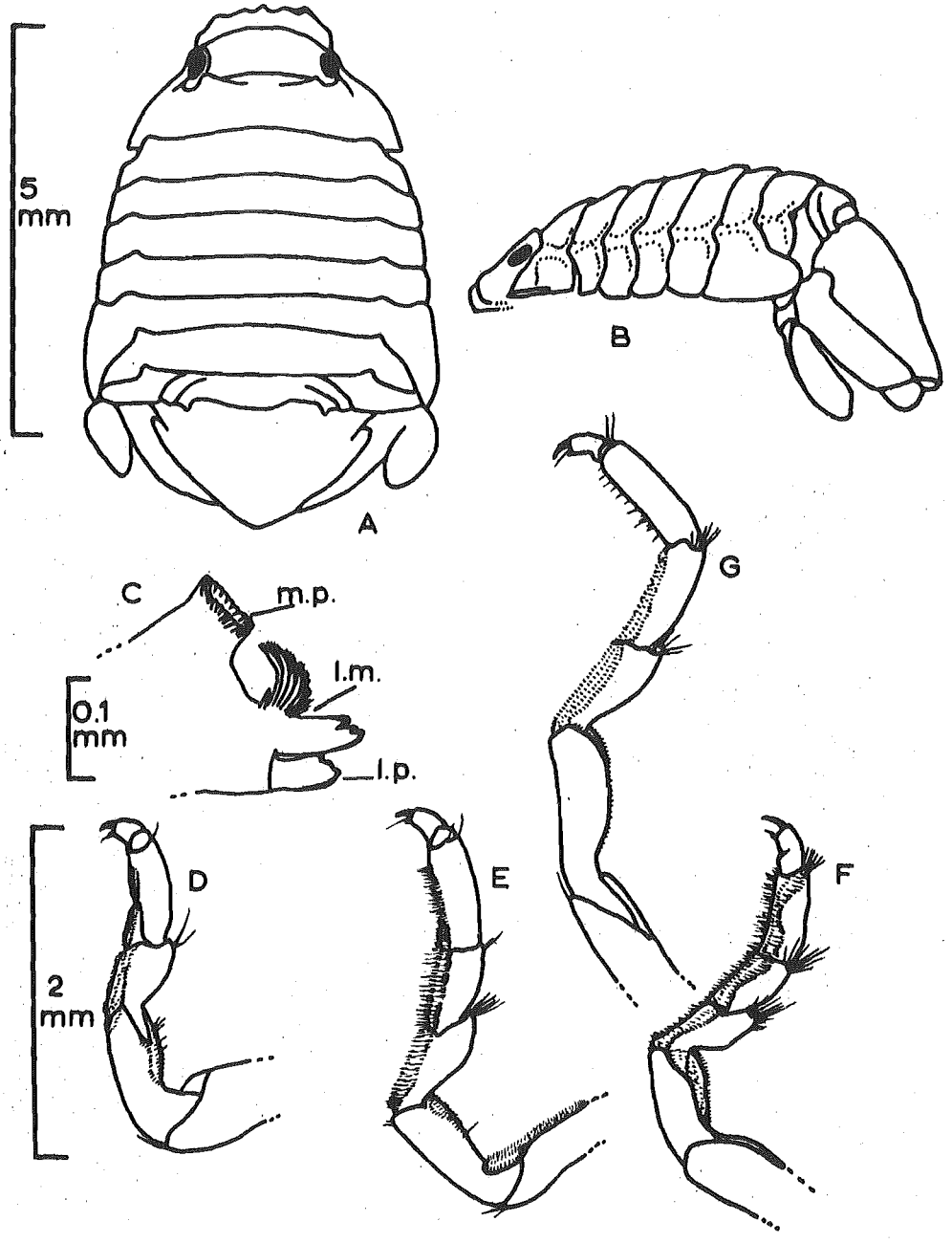
l.m.
right
m.p.
C

Fig. 15

Sphaeroma quoyana

A, B, dorsal and lateral aspects of female; C, mandibles; D, E, F, first, fourth, and seventh thoracic legs.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0.1
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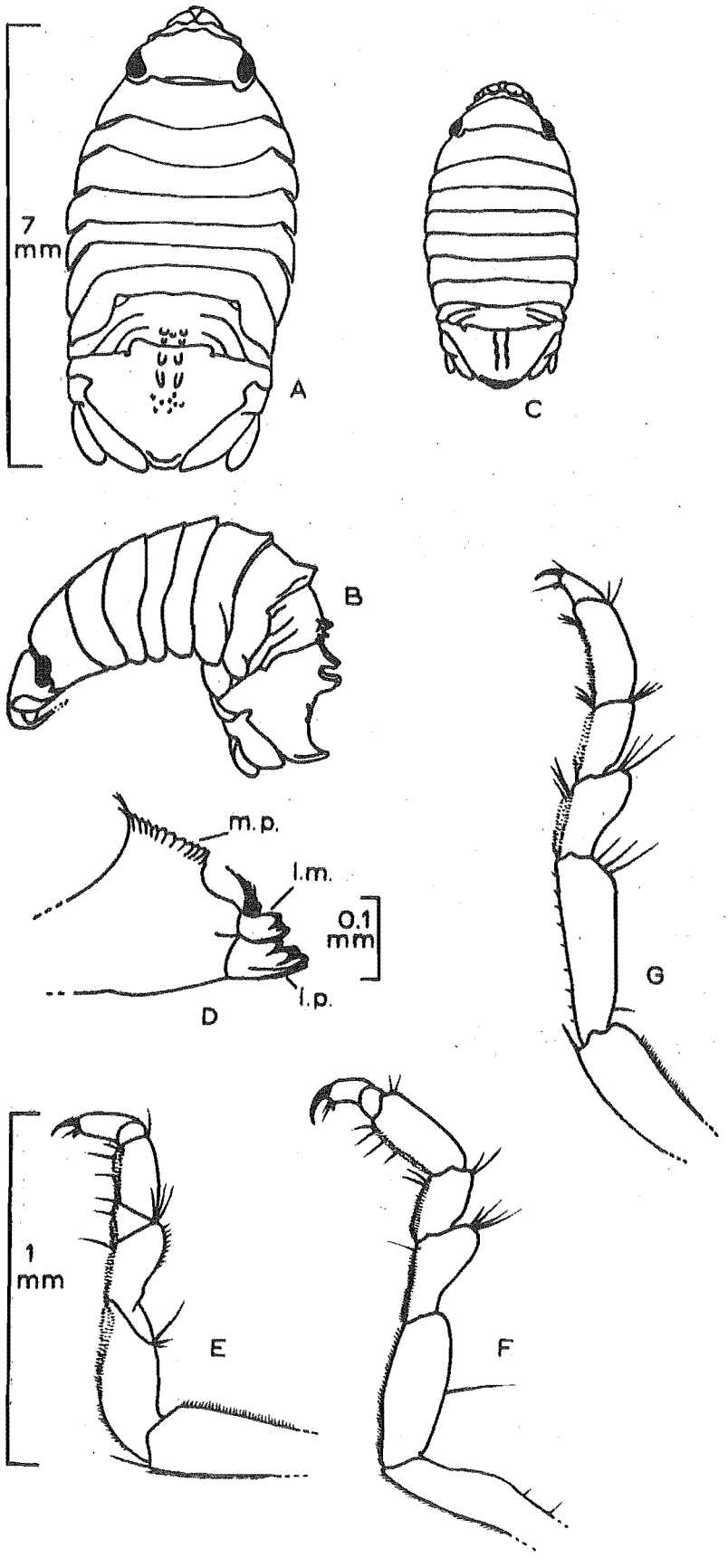
G
D
E
F
2
mm

Fig. 16

Pseudosphaeroma campbellensis

A, B, dorsal and lateral aspects of male; C, left mandible; D, E, F, G, first, second, fourth, and seventh thoracic legs.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1
mm
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F

Fig. 17

Paradynamenopsis crenellata

A, B, dorsal and lateral aspects of male; C, female; D, left mandible; E, F, G, first, fourth, and seventh thoracic legs.

2. Tolerance of temperature, salinity and desiccation

The relationship between temperature and salinity and marine and brackish water animals was reviewed by Kinne (1963, 1964), who pointed out that eurytherm and eurysaline species were more characteristic of coastal, particularly littoral areas. Among species broadly characterised as eurytherm or eurysaline, considerable differences exist in physiological adaptation. Broekhuysen (1940, cited by Moore,1958) demonstrated that upper lethal temperatures and resistance to desiccation were higher in South African littoral gastropods distributed higher on the shores. Riegel (1959) showed that differences in the ability to osmoregulate in species of Gnorimosphaeroma (sphaeromid isopods) agreed with the distribution of the species in bays, estuaries, and freshwater, in California. Todd (1963) demonstrated that temperature and seasonal differences in osmoregulation in the intertidal isopods Ligia oceanica and Idotea granulosa were related to distribution. Naylor (1955a) showed that differences in the ability of British species of Idotea to tolerate salinity changes were again related to differences in the distributions of the species. The inference in all cases is that species with narrower or different ranges of tolerance are prevented from occupying

some intertidal or other habitats by the inability to survive the conditions.

Kinne (1963) pointed out 'Within the same species the biological effects of a given temperature pattern may be different in different [allopatric] populations, at different ages, in different life cycle stages or in the two sexes and may depend on the temperature history of the individual tested, as well as on present or past effects of other environmental factors.' Similar considerations apply to the effects of salinity and desiccation. In the present study, interspecific comparisons were made of physiological tolerances in sympatric populations of several species, to determine the effects of temperature, salinity, and desiccation on ecological, not geographic, distribution. Thus variation among allopatric species-populations does not affect the validity of the comparisons. With respect to differences in effects of temperature and the other factors, and their dependence on the history of the individuals tested, samples of all the rocky shore species tested were collected as nearly as possible at the same time, and were treated identically. Only vigorous and obviously healthy specimens in the middle size range in each species were tested for interspecific comparison; intraspecific comparison was made in the rocky shore species, between the post-embryonic juveniles (see 'Breeding Populations',p. 84)

and larger stages. Possible sources of misleading differences were thus minimised.

Extremes in temperature and salinity were recorded on the shores of the Kaikoura Peninsula in summer and winter (Table 11). Variations conformed to the expected pattern, being greater at higher than at lower intertidal levels, and on more sheltered than on more exposed shores. Although sphaeromids are motile, they are immobilised at low tides, by the absence of continuous water, and so must endure the fluctuations in physical conditions. Species differently distributed vertically and with respect to substrate and wave action thus encounter very different sets of conditions.

Species were tested in the laboratory to compare their tolerances of temperature, salinity, and desiccation, so as to evaluate these as limiting factors.

(i) Lethal Temperatures

Upper lethal temperatures were determined by placing ten freshly collected specimens in sea water of normal salinity (35^{o}/oo), which was heated from room temperature (15 - 18C.) at a constant rate of 1C. per minute, with stirring to ensure uniform oxygen distribution. The temperature at which nine of the ten specimens were dead was

recorded as the upper lethal temperature. Death was indicated by cessation of beating of the pleopods, which first accelerated as the temperature rose, then became irregular, stopping fairly abruptly. No specimen considered dead on this criterion recovered on cooling.

No differences in upper lethal temperature appeared on comparing small ($<$ 3mm) and large specimens in each of the rocky shore species.

No mortality occurred in any species during three days immersion in sea water of normal salinity at 5C., the lowest temperature recorded in any of the collecting areas.

Upper lethal temperatures (Table 12) ranged from 40 - 42C. in the species of less exposed rocky shores and brackish water, down to 30 - 31C. in species of more exposed rocky shores and lower intertidal levels. The temperatures recorded in summer on less exposed (class III and IV) shores ranged from 15 to 33C. (Table 11), exceeding the lethal temperatures of only four of the eight species of more exposed shores. Maximum temperatures on more exposed (class I and II) shores in summer and on all shore classes in winter were lower than the upper lethal temperatures in all species.

Differences in survival after 24 hours immersion at 30C. in sea water of normal salinity indicate that temperature alone is an effective limiting factor. None in the species of more exposed rocky shores (Isocladus

magellanicus and Cymodocella tubicauda, living among stones; all algal-cryptic and algal-frond species) survived. In all the species of more sheltered shores (I. armatus and Exosphaeroma obtusa, living among stones; all the brackish water species), 80% or more survived. Species of the more exposed shores are thus unable to survive the temperatures of the higher levels and less exposed shores in summer, although these may be several degrees below the upper lethal temperatures.

In all species, 100% survived after 24 hours immersion in normal sea water at 20C. The limiting effect of temperature alone is thus confined to the summer months.

(ii) Temperature and Salinity

Tolerances of temperature and salinity were compared by immersing ten freshly collected specimens for 24 hours in 500 ml of sea water ranging in salinity from 0 °/oo to 70 °/oo (0 - 200%), at 10, 20, and 30C. To prepare the range of salinities, sea water of normal salinity was diluted with distilled water, or concentrated by evaporation. Temperatures were controlled by water baths, and salinities were maintained at the higher temperatures by periodic topping up to a mark with

distilled water at the same temperature. Before survivors were counted, the water was restored to room temperature and normal salinity over a period of 30 minutes, to allow for any recovery.

No differences in tolerance were found in specimens of more and less than 3 mm length in any of the rocky shore species. Results are given in Table 13a, b, c, and d. In this study, species are considered to 'tolerate' conditions if 80% or more survive after 24 hours (see also Naylor, 1955a).

Interaction between temperature and salinity is clearly evident. In each species, the salinity tolerance is greatest at 10C., less at 20 and 30C. Conversely, temperature tolerance is lower in salinities lower and higher than normal.

At the lowest temperature, 10C., salinity tolerances differ widely, increasing from 50 - 100% sea water (18 - 35 $^{o}/oo$) in Amphoroidea falcifer to 0 - 200% (0 - 70 $^{o}/oo$) in Pseudosphaeroma campbellensis. The narrowest ranges of salinity tolerance occur in the rocky shore species Scutuloidea maculata and Amphoroidea falcifer, least exposed to wide fluctuations, living on algal fronds on exposed shores. Tolerances are wider in the algal-cryptic species, being broadest in Dynamenella cordiforaminalis, distributed highest and most widely in this group, and narrowest in D. hirsuta, restricted to exposed shores. In

the group living among stones, the range in the two more exposed species, Isocladus magellanicus and Cymodocella tubicauda, is similar to that in the exposed algal-cryptic species, Dynamenella huttoni and D. hirsuta. The range is wider in Exosphaeroma obtusa, distributed higher and on less exposed shores, and widest in Isocladus armatus, the rocky shore species with the highest vertical distribution on the least exposed shores. In the two brackish water species tested, the salinity ranges are equal, but Pseudosphaeroma campbellensis tolerates 0 - 175% sea water, Paradynamenopsis crenellata 6.25 - 200%. The correlation with distribution is clear, Pseudosphaeroma living in and near to the fresh water flow, Paradynamenopsis living in situations in which they are submerged only at high tides in mixed fresh and sea water.

Thus variations in the range in salinity tolerance at 10C. are directly related to the variation in salinity encountered by each species in its particular part of the environment.

At the higher temperatures, 20 and 30C., the salinity tolerances are reduced in all species. The effects of the temperature-salinity interaction vary again with the species distributions. In the rocky shore species, tolerances narrow symmetrically about 35 $^{o}/_{oo}$ (100% sea water); thus the species which are eurysaline at low temperatures tend to become stenosaline at higher temp-

eratures. In the brackish water species on the other hand, tolerance of high salinities is reduced more than that of low salinities; thus these eury- or holeurysaline species tend to become oligostenosaline at higher temperatures.

The ecological consequences of the temperature-salinity interaction are clear. Exosphaeroma obtusa for example overlaps widely with Isocladus armatus, both horizontally and vertically, and is widely tolerant of variations in salinity at 10C. (25 - 200% sea water), but less so at 20C. (50 - 175%), and at 30C. is reduced to 80% survival in only 100% sea water. E. obtusa is obviously prevented from occupying higher vertical levels on less exposed shores by its inability to survive in the combined conditions of temperature and salinity (class IV shores, Table 11). Similarly, Isocladus armatus tolerates the same range of salinities, 6.25 - 200% sea water, as the brackish water Paradynamenopsis crenellata at 10C., but is limited to 12.5 - 175% at 20C., and to 50 - 150% at 30C. At 30C., P. crenellata still tolerates 12.5 - 150% sea water. Thus although I. armatus may inhabit the vicinity of fresh or brackish water, it is prevented from extending its ecological range by inability to survive in low salinities at high temperatures.

The suggestion was made (p. 38) that juveniles of Dynamenella huttoni suffered heavy losses because of dis-

placement from lower and more exposed situations to which adults are restricted, to higher and less exposed Corallina officinalis. This suggestion can now be supported by evidence from the temperature-salinity tests. The thermal death point in D. huttoni is 30C., compared with 35C. in D. cordiforaminalis, living predominantly in C. officinalis at the same levels (up to HWN). D. huttoni tolerates 50 - 175% sea water at 10C. and 50 - 100% at 20C., compared with 25 - 200% at 10C. and 25 - 175% at 20C. in D. cordiforaminalis. Thus the juveniles of D. huttoni are less fitted for survival in this part of the environment than both adults and juveniles of D. cordiforaminalis. Temperature and salinity at HWN class I shores (Table 11) vary beyond the range which D. huttoni can tolerate for 24 hours in the laboratory, and must therefore kill the juveniles which are abundant at this level on these shores (see also 'Breeding Populations' p. 92).

(iii) Desiccation

After removal of excess moisture with filter paper, ten individuals of each species were placed separately in constant humidity chambers at 10, 20, and 30C., for 24 hours. Relative humidities of 100% and 70% were maintained

by moist filter paper and sulphuric acid solutions (Hale, 1958).

Specimens in the middle size range in each species were used for interspecific comparisons. The results (Table 14) show that the species vary greatly in their ability to resist desiccation.

At 10C. and 100% relative humidity, 100% survived in all species except Scutuloidea maculata (50%) and Amphoroidea falcifer (80%), algal-frond species living at and below LWN on exposed shores, rarely exposed to the air.

In the rocky shore species, specimens of less than 3 mm were also tested. At 10C. and 100% relative humidity, no survival occurred in any species except 20% in Isocladus armatus.

At 10C. and 70% relative humidity the trend appears to be modified by differences in size, but is clear in the species living among stones. The greatest sample mean length in Isocladus armatus was 5.4 mm, compared with 9.1 mm in Exosphaeroma obtusa and 7.7 mm in Isocladus magellanicus. But in the smaller species, I. armatus, 100% survived the reduced humidity, compared with 85% in E. obtusa and 65% in I. magellanicus. Thus both adults and juveniles of I. armatus are superior to the other rocky shore species in resisting desiccation.

In the algal-cryptic rocky shore species, survival was higher in the two larger, Dynamenopsis varicolor and Dynamenella huttoni. In the smaller of the two remaining species, Dynamenella cordiforaminalis (mean length 4.5 mm), survival was slightly higher (70%) than in the larger, D. hirsuta (mean length 6.25 mm) (60%). D. cordiforaminalis live predominantly among shrubby Corallina officinalis and are often exposed to the air. D. hirsuta on the other hand live exclusively in the tunnelled holdfasts of Durvillea antarctica, seldom exposed to the air. Thus again the greater resistance in spite of the smaller size is related to the species distribution.

In the algal-frond species Scutuloidea maculata and Amphoroidea falcifer, there were no survivors in the reduced humidity.

At higher temperatures, 20 and 30C., no survivors occurred in any of the rocky shore species in either 100% or 70% relative humidity.

In the brackish water species, Pseudosphaeroma campbellensis resisted desiccation to about the same extent as the exposed rocky shore species, 100% and 60% surviving in 100% and 70% relative humidity respectively at 10C., no survivors at 20 or 30C. P. campbellensis live in continuously wet conditions under stones, and are very seldom exposed to air. Paradynamenopsis crenellata on the other hand live among clusters of Mytilus hanging from

wooden structures at MTL, which are drained and exposed to air on every tide. Resistance to desiccation in P. crenellata is very much higher than in any other species, indicated by survival of 90% and 75% respectively at 20C. in relative humidities of 100% and 70%, and of 35% at 30C. in 100% relative humidity.

Naylor (1955a) found no appreciable differences in resistance to desiccation in sublittoral, littoral, and brackish water species of Idotea, and concluded that 'exposure to the air is an absolute limiting factor for all species, and that it is some factor other than tolerance of exposure to the air which allows the shore species to inhabit the intertidal zone which the other species seem unable to colonize'. Considering only the algal-inhabiting species of Sphaeromidae, the same conclusion appears to hold. Considering the rocky shore and brackish water species together however, obviously adaptive differences appear. Thus both of the two algal-frond species are less resistant than any other rocky shore species, and are therefore restricted to low levels. In Isocladus armatus both adults and juveniles are superior in resistance to the remaining rocky shore species, which are thus limited in vertical distribution. Paradynamenopsis crenellata alone of the species studied survived in large numbers in both 100% and 70% relative humidity at

20C., and also in small numbers in 100% relative humidity at 30C. A degree of resistance to desiccation thus enables some sphaeromid species to occupy habitats which are denied to others by their inability to survive.

Table 11. Extremes of temperature and salinity on rocky shores of the Kaikoura Peninsula: a. summer (February); b. winter (July).

a.		Class I shores		Class IV shores		
		HWN	sublittoral	HWS	HWN	sub-littoral
Temperature, C.	maximum	28	16	33	33	17
	minimum	14	14	15	15	15
Salinity, °/oo	maximum	41	35	>75	65	36
	minimum	35	35	36	36	35
b.						
Temperature, C.	maximum	11	10	14	14	11
	minimum	7	8	5	5	8
Salinity, °/oo	maximum	35	35	35	35	35
	minimum	27	35	3	18	35

Table 12. Thermal death points of intertidal Sphaeromidae.

a. Species living among stones	Summer	Winter
I. armatus ('std')	40C.	36C.
E. obtusa	37	36
I. magellanicus	35	35
C. tubicauda	35	33
b. Algal-cryptic species		
D. cordiforaminalis	35	35
D. varicolor	35	34
D. huttoni	30	29
D. hirsuta	32	
c. Algal-frond species		
S. maculata	30	28
A. falcifer	31	28
d. Brackish water species		
S. quoyana	42	
P. campbellensis	42	
P. crenellata	42	

Table 13. Tolerance of temperature and salinity in intertidal Sphaeromidae after 24 hours immersion in sea water from 0 to 200% concentration, at 10, 20, and 30C.; a. species living among stones; b. algal-cryptic species; c. algal-frond species; d. brackish water species.

a.

salinity, °/oo	0	2.2	4.4	9	18	35	53	61	70	Temp.C.
concentration, %	0	6.25	12.5	25	50	100	150	175	200	
I. armatus ('std')	0	100	100	100	100	100	100	100	100	10
	0	50	80	100	100	100	100	100	10	20
	0	0	0	20	100	100	90	50	0	30
E. obtusa	0	10	50	100	100	100	100	100	80	10
	0	0	0	30	100	100	100	90	0	20
	0	0	0	0	0	80	0	0	0	30
I. magellanicus	0	0	10	70	100	100	100	90	80	10
	0	0	0	40	100	100	90	70	0	20
	0	0	0	0	0	0	0	0	0	30
C. tubicauda	0	0	0	70	100	100	100	100	0	10
	0	0	0	30	100	100	100	100	0	20
	0	0	0	0	0	0	0	0	0	30

Table 13 continued

salinity, °/oo	0	2.2	4.4	9	18	35	53	61	70	Temp.C.
concentration, %	0	6.25	12.5	25	50	100	150	175	200	
b.										
D. cordiforaminalis	0	0	10	90	100	100	100	100	100	10
	0	0	0	80	80	100	100	100	0	20
	0	0	0	0	0	0	0	0	0	30
D. varicolor	0	0	20	80	100	100	100	100	0	10
	0	0	0	40	90	100	100	80	0	20
	0	0	0	0	0	0	0	0	0	30
D. huttoni	0	0	50	70	100	100	100	100	0	10
	0	0	0	70	90	100	50	0	0	20
	0	0	0	0	0	0	0	0	0	30
D. hirsuta	0	0	0	60	100	100	100	100	0	10
	0	0	0	40	90	100	80	0	0	20
	0	0	0	0	0	0	0	0	0	30

Table 13 continued.

salinity, °/oo	0	2.2	4.4	9	18	35	53	61	70	Temp.C.
concentration, %	0	6.25	12.5	25	50	100	150	175	200	
c.										
S. maculata	0	0	0	0	100	100	100	40	0	10
	0	0	0	0	30	100	70	0	0	20
	0	0	0	0	0	0	0	0	0	30
A. falcifer	0	0	0	0	90	100	60	0	0	10
	0	0	0	0	30	100	50	0	0	20
	0	0	0	0	0	0	0	0	0	30
d.										
P. campbellensis	80	100	100	100	100	100	100	100	50	10
	0	100	100	100	100	100	100	80	20	20
	0	60	100	100	100	100	20	0	0	30
P. crenellata	0	100	100	100	100	100	100	100	100	10
	0	100	100	100	100	100	100	100	100	20
	0	40	80	80	100	100	80	60	20	30

Table 14. Resistance to desiccation in intertidal Sphaeromidae: percentage survival after 24 hours at 100% and 70% relative humidity at 10, 20, 30C.; a. species living among stones; b. algal-cryptic species; c. algal-frond species; d. brackish water species.

Temperature, C.	10		20		30	
Relative humidity, %	100	70	100	70	100	70
a.						
I. armatus	100	100	0	0	0	0
E. obtusa	100	85	0	0	0	0
I. magellanicus	100	65	0	0	0	0
C. tubicauda	100	25	0	0	0	0
b.						
D. cordiforaminalis	100	70	0	0	0	0
D. varicolor	100	100	0	0	0	0
D. huttoni	100	90	0	0	0	0
D. hirsuta	100	60	0	0	0	0
c.						
S. maculata	50	0	0	0	0	0
A. falcifer	80	0	0	0	0	0
d.						
P. campbellensis	100	60	0	0	0	0
P. crenellata	100	90	90	75	35	0

3. Breeding Populations

Previous studies of breeding populations of Sphaeromidae appear to be limited to Sphaeroma hookeri in Kiel Harbour (Kinne 1954) and in Copenhagen Harbour (Jensen 1955). Populations of nine species were studied on the rocky shores of the Kaikoura Peninsula to compare breeding patterns in relation to ecological distribution.

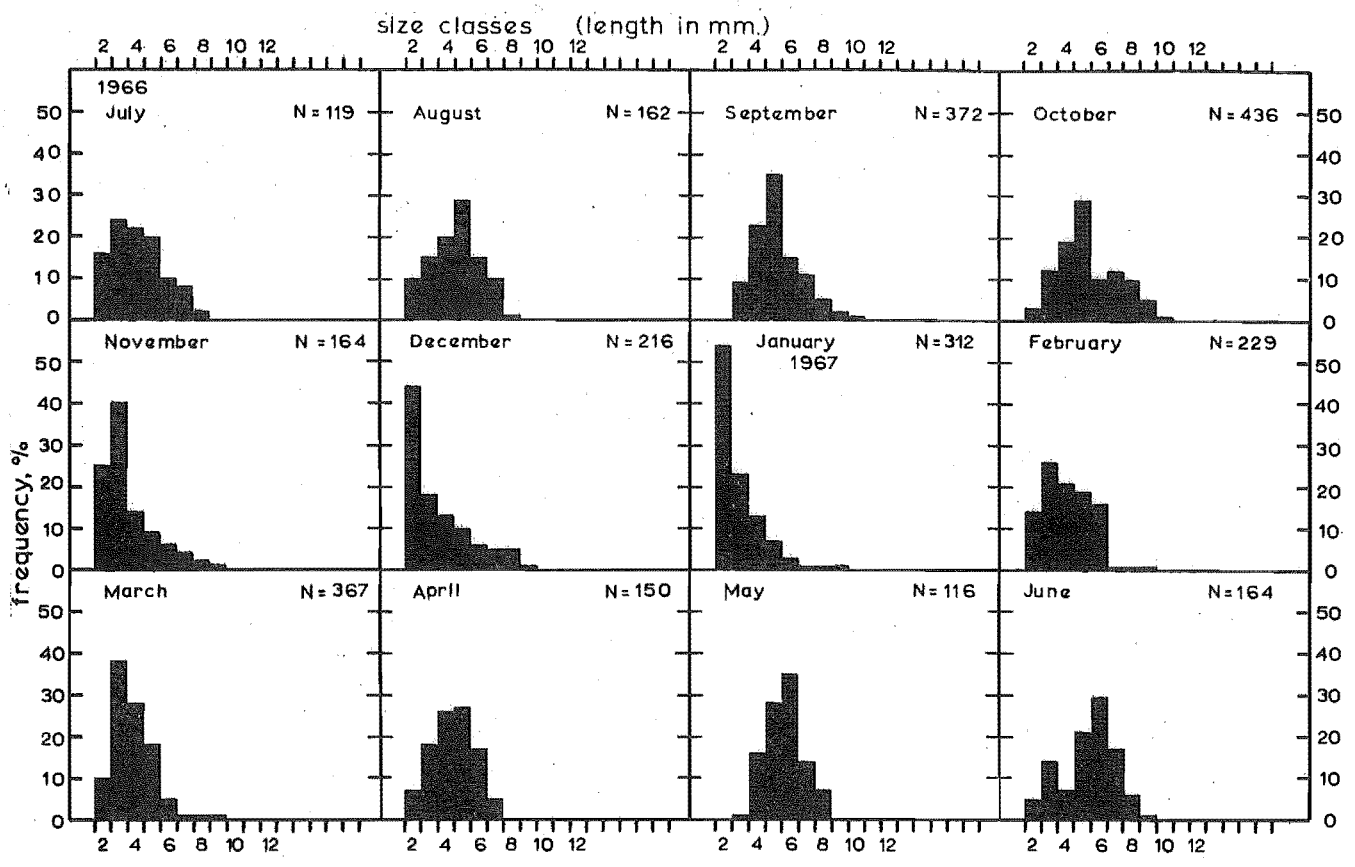
Materials and methods

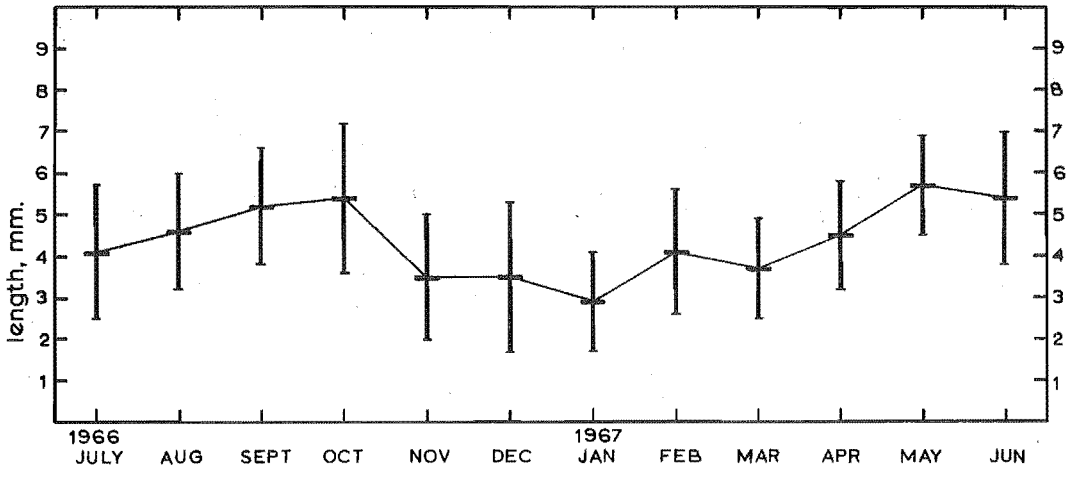
Monthly samples were taken from July 1966 to June 1967, each species being sampled on the class of shore on which it was most abundant. All parts of each shore were searched to minimise bias from differences in distribution of sizes or sexes, all specimens of one species being combined into one sample, killed and preserved in 5% formalin in sea water. Very large samples were subdivided by spreading specimens under water in a dish, gently decanting the water, and progressively halving the sample to 100-300 specimens (see also Naylor 1955a).

Each specimen was measured under a binocular microscope fitted with a graduated eyepiece accurate to 0.1 mm. Within each species the specimens were grouped into size classes with intervals of 0.5 mm in the species 7 mm or less in length, and of 1.0 mm in species more than 7 mm long. The measured specimens were further grouped in the following

categories relative to breeding and development:

post-embryonic juveniles	- prior to full development of the 7th pereonal segment and pereopods
pre-adult juveniles	- 7th pereonal segment and pereopods fully developed but sex indeterminable from externals
males	- penes visible
non-gravid females	- oostegites present, either rudimentary or fully developed, eggs still in ovaries
gravid females	- eggs (or embryos) in brood sacs.





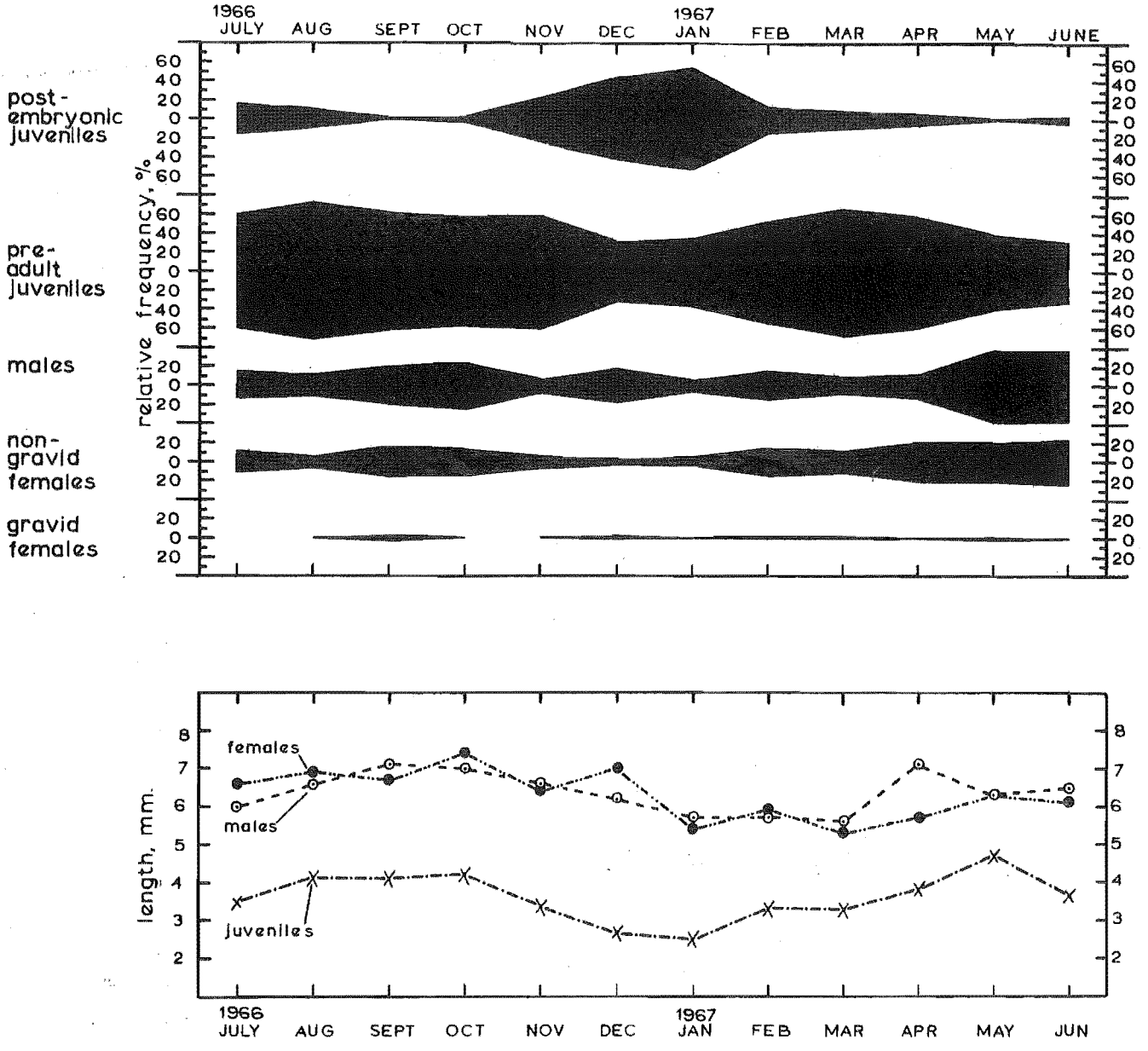
Isocladus armatus

Figure 18

Percentage frequency of Isocladus armatus in each size class (1 mm), in monthly samples taken from July 1966 to June 1967 at Wairepo Flat, Kaikoura (class IV shore).

Figure 19

Mean lengths and SDs of samples of I. armatus taken as in Fig. 18.



Isocladus armatus

Figure 20

Changes in the breeding structure of a population of Isocladus armatus, from monthly samples taken as in Fig. 18.

Figure 21

Mean lengths of juveniles, males, and females of I. armatus, from samples taken as in Fig. 18.

a. Species living among stones

1. Isocladus armatus

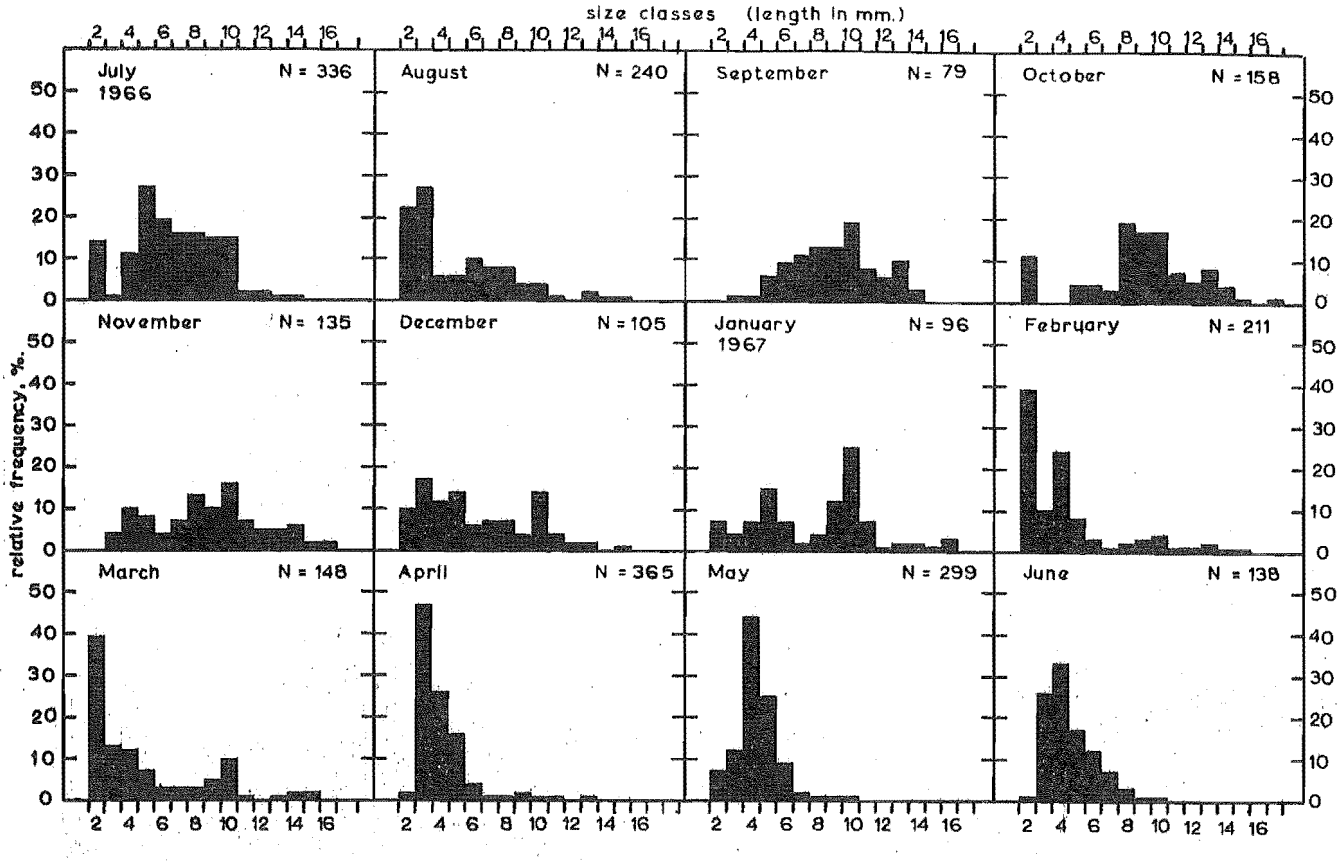
Monthly samples were taken on a class IV shore (Wairepo Flat). Relative abundance was consistently high, fluctuating between 700 and 1000 m^{-2} from November to April with a maximum of 3600 m^{-2} in January, falling back below 1000 m^{-2} in May and June.

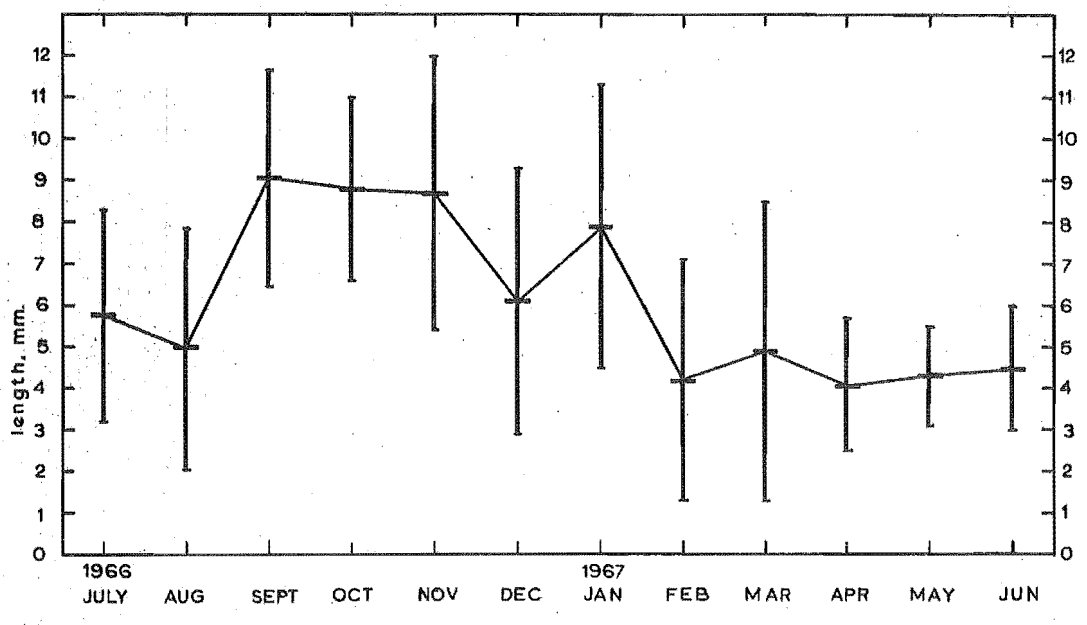
From July to October, frequencies of the 2 mm class (Fig. 18) fell, while maximum length rose from 8 to 10 mm, and the sample mean size (Fig. 19) increased; these samples comprised small and decreasing proportions of post-embryonic juveniles, large numbers of pre-adult juveniles which decreased after August, and males and females in relatively small proportions (Figs 20, 21). From November to January the size range was constant from 2 to 9 mm, but increasing proportions of post-embryonic juveniles (Fig. 20) reached a maximum in January, after which the larger males and females disappeared (Figs. 18, 21). The February and March samples again consisted largely of pre-adult juveniles, sharply reduced numbers of post-embryonic juveniles, and small males and females hatched earlier in the summer. From April to June, maximum size increased from 7 to 9 mm, frequencies and mean sizes of males and females increasing as the young released earlier in the year grew and developed.

Sample mean size increased from April to May as frequencies of the smaller classes diminished, but decreased with the reappearance of 2 mm post-embryonic juveniles in the June sample.

Two prolonged breeding cycles were apparent. A winter cycle from June to August with a small peak in July was evidently produced by individuals released earlier in the preceding summer and maturing during the autumn. A summer cycle from October to April with a large peak in January appeared to be produced by two main groups. First, individuals released late in the preceding summer which grew during the winter and matured at larger sizes in the spring then produced young earlier in the summer. Second, individuals released in the winter cycle which grew during the spring and matured at smaller sizes then produced young later in the summer.

Proportions of gravid females were consistently lower, but those of post-embryonic juveniles were larger than in the other species living among stones but in situations more exposed to wave action (Table 17).





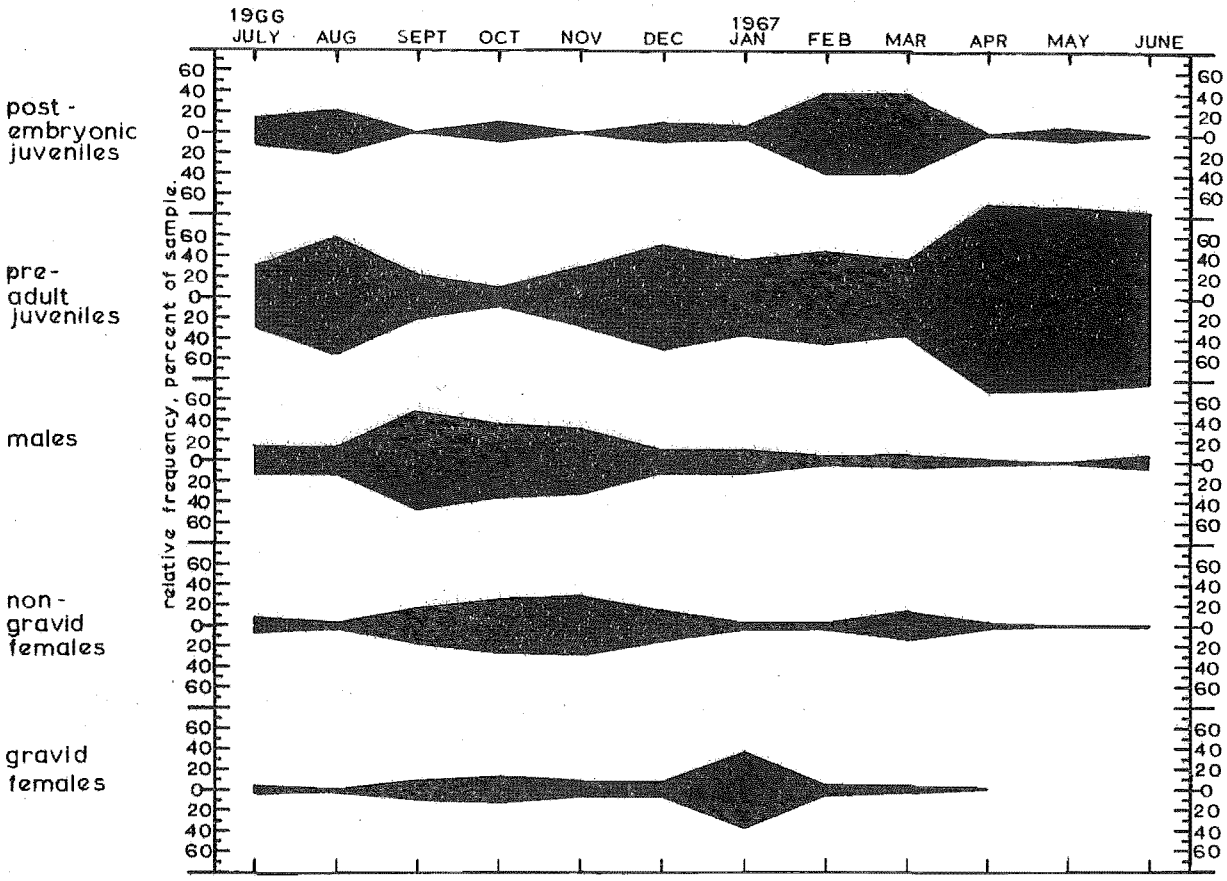
Exosphaeroma obtusa

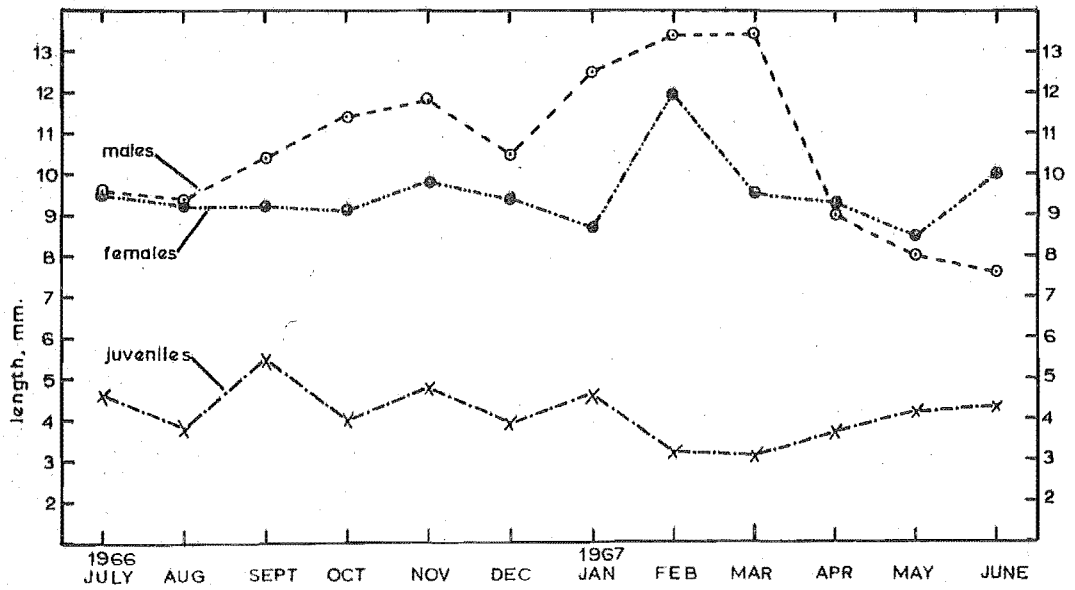
Figure 22

Percentage frequency of Exosphaeroma obtusa in each size class (1 mm), in monthly samples taken from July 1966 to June 1967 at Whaler's Bay, Kaikoura (class III shore).

Figure 23

Mean lengths and SDs of samples of E. obtusa taken as in Fig. 22.





Exosphaeroma obtusa

Figure 24

Changes in the breeding structure of a population of Exosphaeroma obtusa, from monthly samples taken as in Fig. 22.

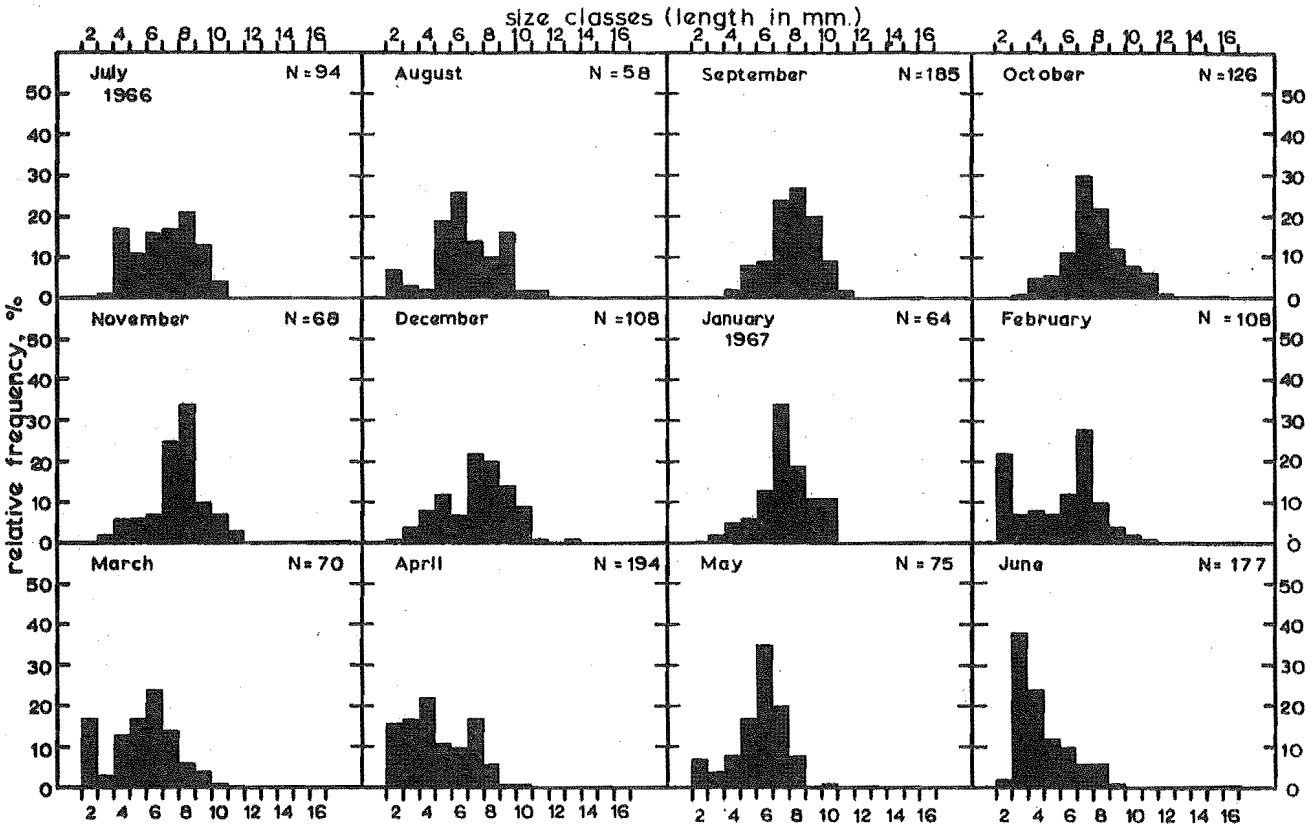
Figure 25

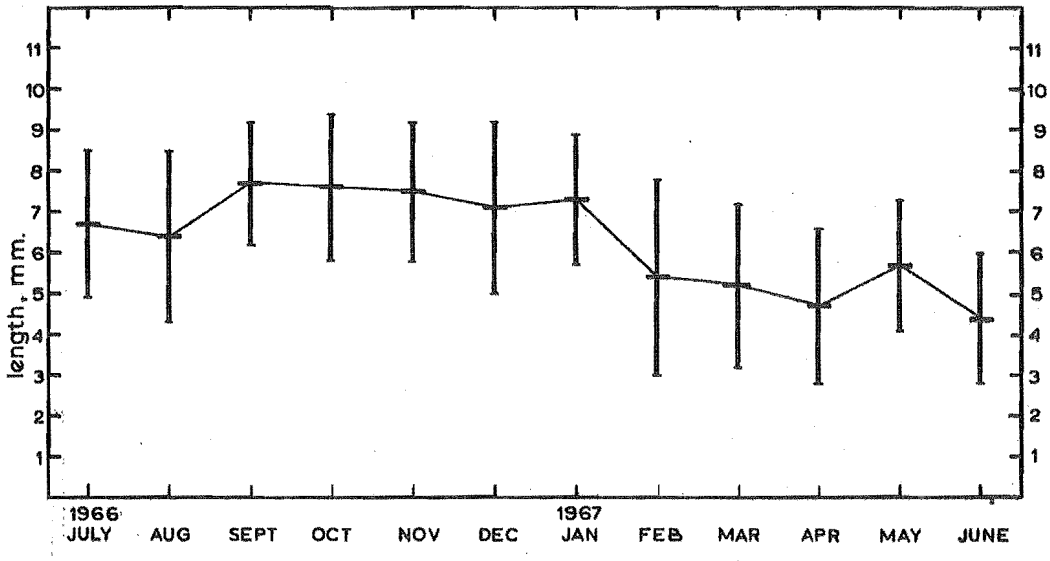
Mean lengths of juveniles, males, and females of E. obtusa, from samples taken as in Fig. 22.

2. Exosphaeroma obtusa

Monthly samples were taken on a class III shore (Whaler's Bay). In July and August the bulk of the samples comprised pre-adult juveniles, with small proportions of males and females and post-embryonic juveniles (Fig. 24). In these months, mean lengths of the samples (Fig. 23) and of males and females (Fig. 25) were low, but increased from August to January while growth and development continued. In February and March, large numbers of post-embryonic juveniles appeared (Fig. 24), sample mean lengths falling sharply (Fig. 23); maximum lengths (Fig. 22) and mean lengths of males and females (Fig. 25) fell sharply from March, indicating the disappearance of the larger adults after breeding. From April, the samples again largely consisted of pre-adult juveniles, sample mean lengths gradually increasing with growth to June (Fig. 23).

Two breeding cycles are again indicated, by the small increase in post-embryonic juveniles in winter (July and August) and the large increase in summer (February and March). Proportions of gravid females were consistently higher than in I. armatus but those of post-embryonic juveniles were lower (Table 17).





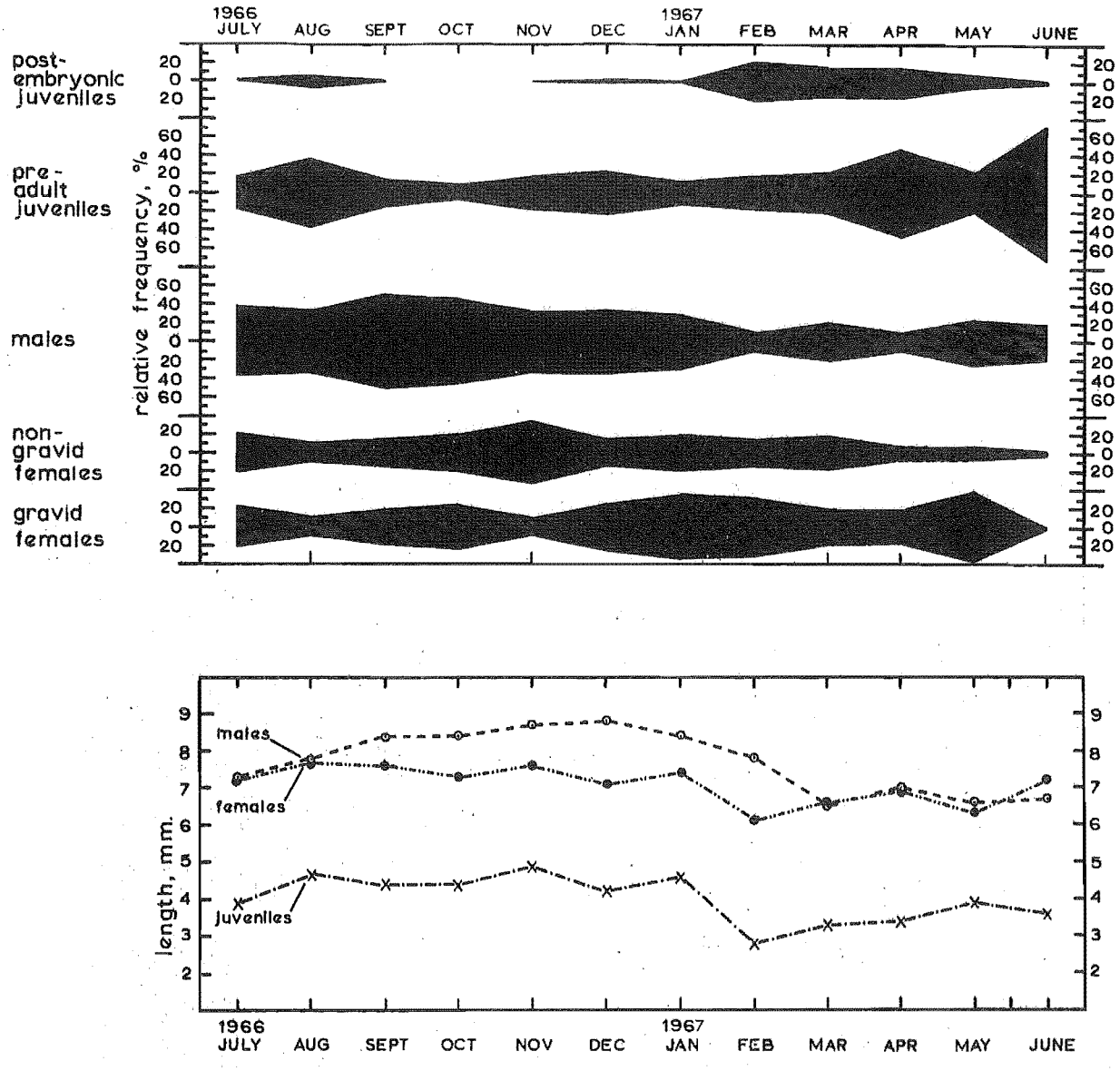
Isocladus magellanicus

Figure 26

Percentage frequency of Isocladus magellanicus in each size class (1 mm), in monthly samples taken from July 1966 to June 1967 at Whaler's Bay, Kaikoura (class III shore).

Figure 27

Mean lengths and SDs of samples of I. magellanicus taken as in Fig. 26.



Isocladus magellanicus

Figure 28

Changes in the breeding structure of a population of Isocladus magellanicus, from monthly samples taken as in Fig. 26.

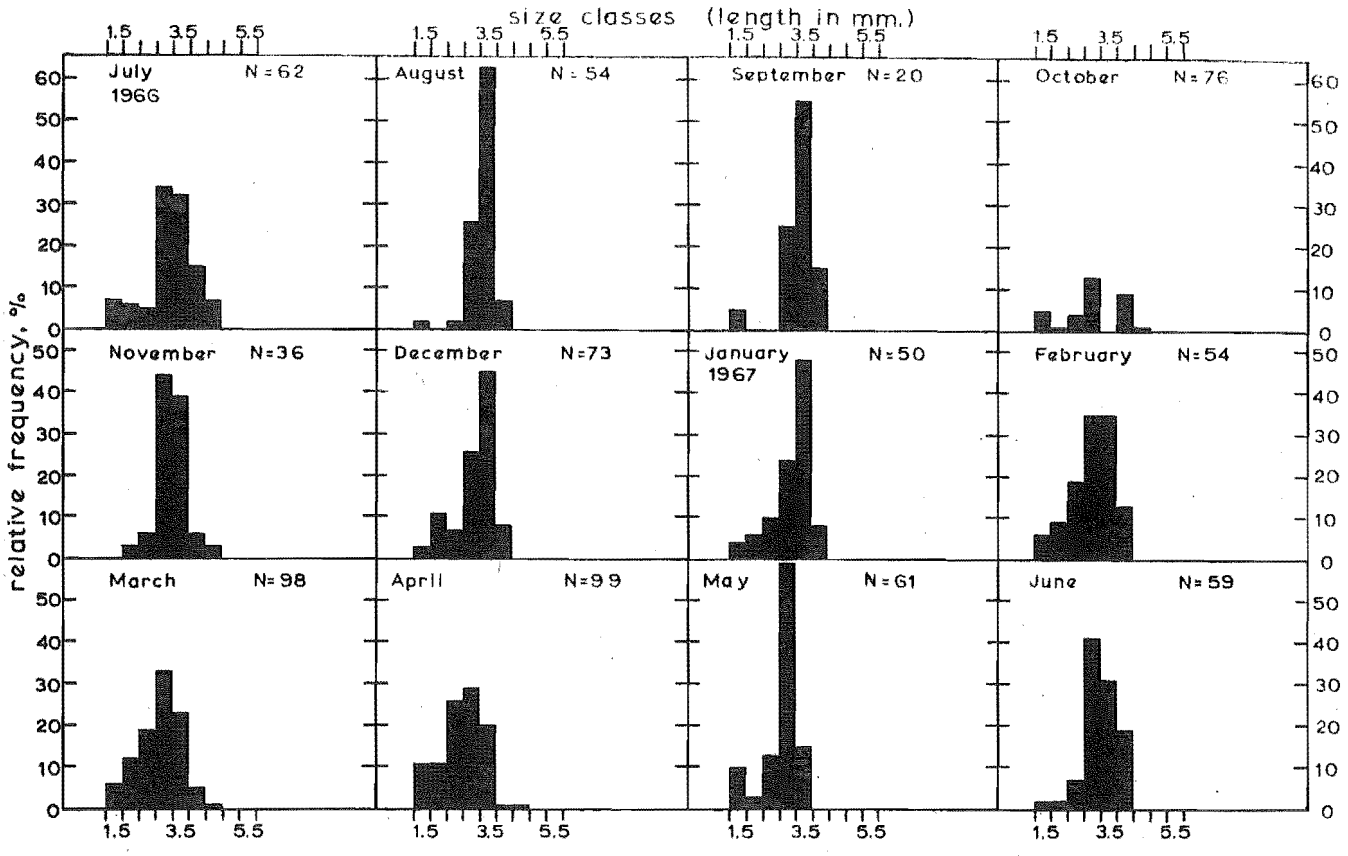
Figure 29

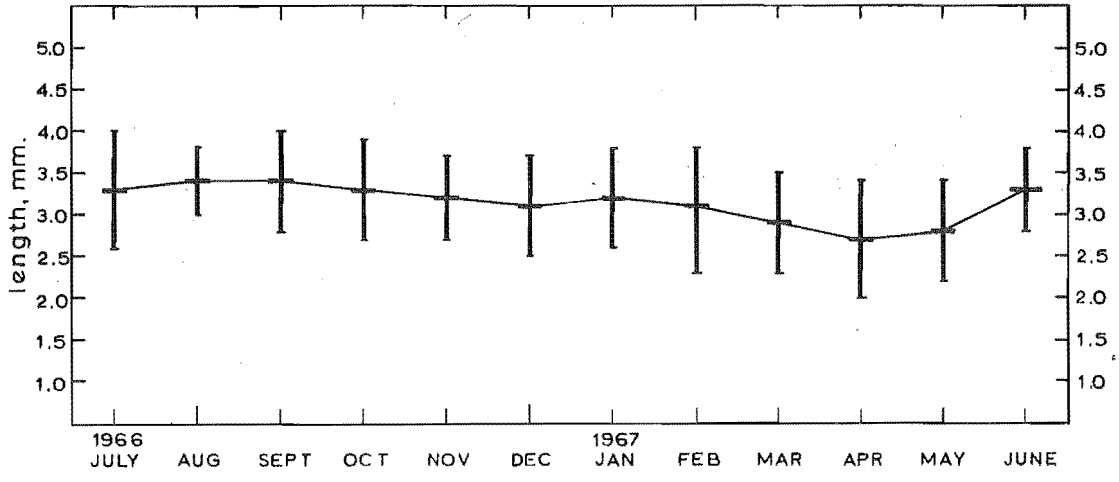
Mean lengths of juveniles, males and females of I. magellanicus, from samples taken as in Fig. 26.

3. Isocladus magellanicus

Monthly samples were taken on a class III shore (Whaler's Bay). Maximum size and frequencies in the lower classes (Fig. 26) increased from July to September, together with sample mean lengths (Fig. 27) in which a small dip in August was produced by the appearance of a small number of young (Fig. 28). Development together with a small amount of breeding continued until January. In February, March, and April, larger numbers of post-embryonic juveniles appeared, causing a sharp fall in sample mean lengths; during these months the mean lengths of males and females (Fig. 29) decreased as the larger classes (Fig. 26) disappeared after breeding, and as smaller animals matured.

Two breeding cycles are again apparent from the increases in post-embryonic juveniles in August and in February, March, and April, but young were effectively present throughout the year, at least in small numbers. Compared with I. armatus and E. obtusa, smaller proportions of pre-adult juveniles and large proportions of males and females indicated relatively rapid development (Figs 20, 24, 28). Greater proportions of gravid females but smaller proportions of post-embryonic juveniles occurred than in the two preceding species (Table 17), indicating increases in both breeding and juvenile mortality, associated with greater exposure to wave action.





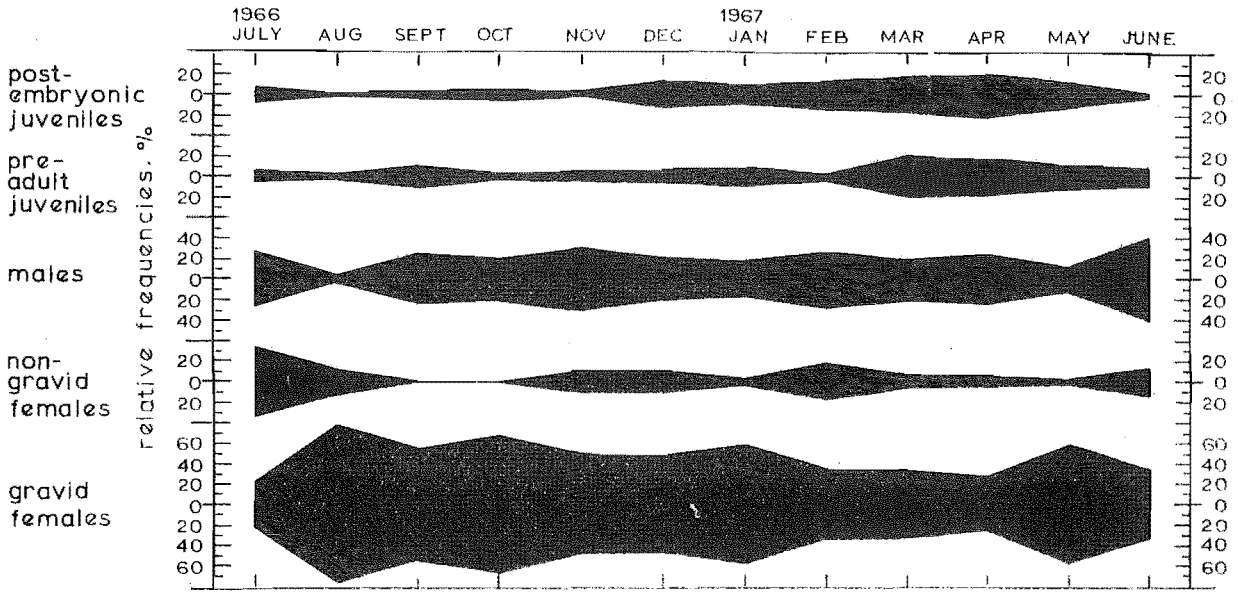
Cymodocella tubicauda

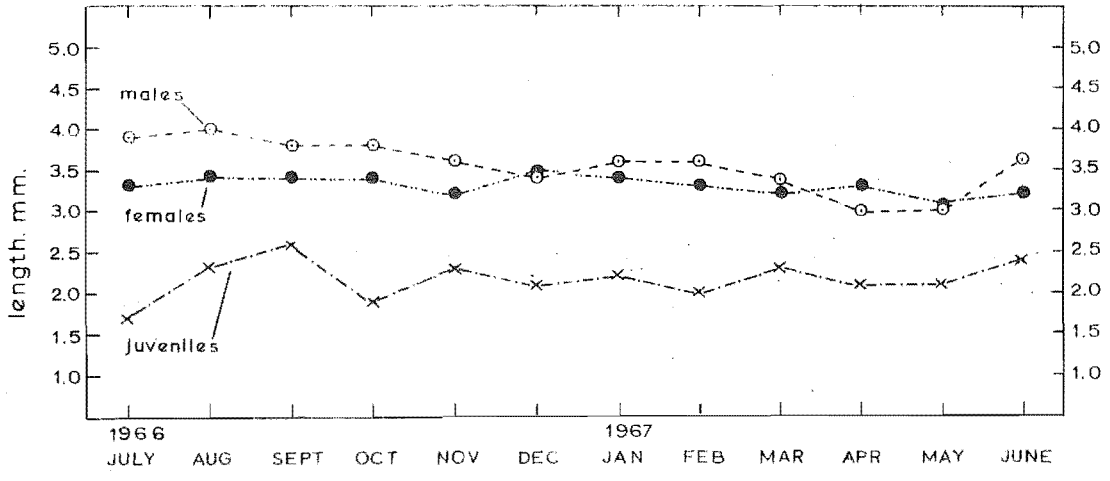
Figure 30

Percentage frequency of Cymodocella tubicauda in each size class (0.5 mm), in monthly samples taken from July 1966 to June 1967 at Whaler's Bay, Kaikoura (class III shore).

Figure 31

Mean lengths and SDs of samples of C. tubicauda taken as in Fig. 30.





Cymodocella tubicauda

Figure 32

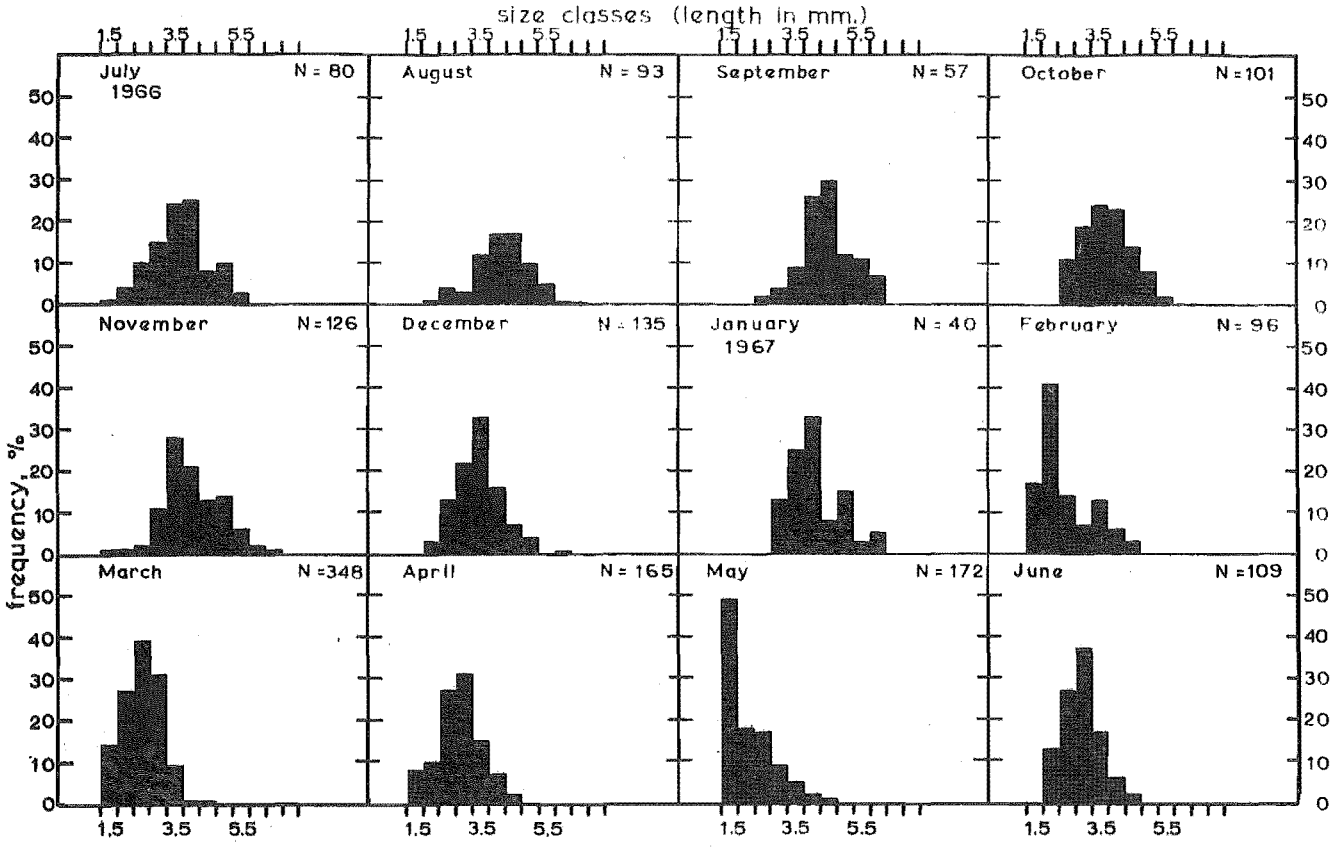
Changes in the breeding structure of a population of Cymodocella tubicauda, from monthly samples taken as in Fig. 30.

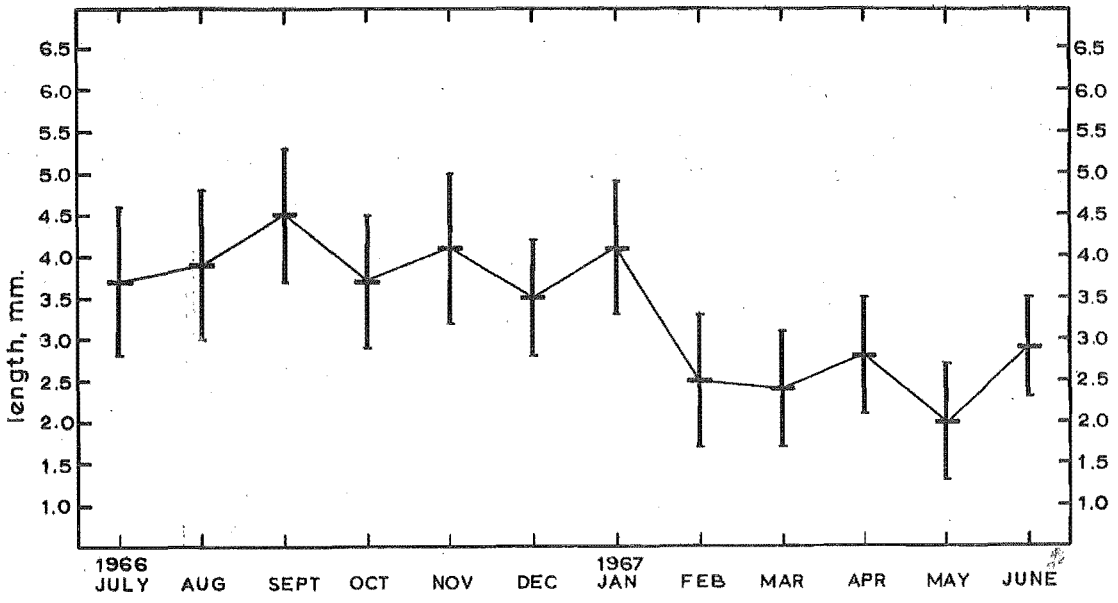
Figure 33

Mean lengths of juveniles, males and females of C. tubicauda, from samples taken as in Fig. 30.

4. Cymodocella tubicauda

Monthly samples of C. tubicauda were taken on a class III shore (Whaler's Bay). Post-embryonic juveniles were present throughout the year (Fig. 32), in small proportions from July to November, increasing from December to April. The small proportions of post-embryonic juveniles relative to the large proportions of gravid females indicate heavy juvenile mortality, and the small proportions of pre-adult juveniles suggest rapid development. The large proportions of gravid females in all samples indicate continuous breeding. Little change is evident in the mean lengths of the monthly samples (Fig. 31) or of juveniles, males, and females (Fig. 33), indicating that the population is stable, breeding development and mortality being in equilibrium.





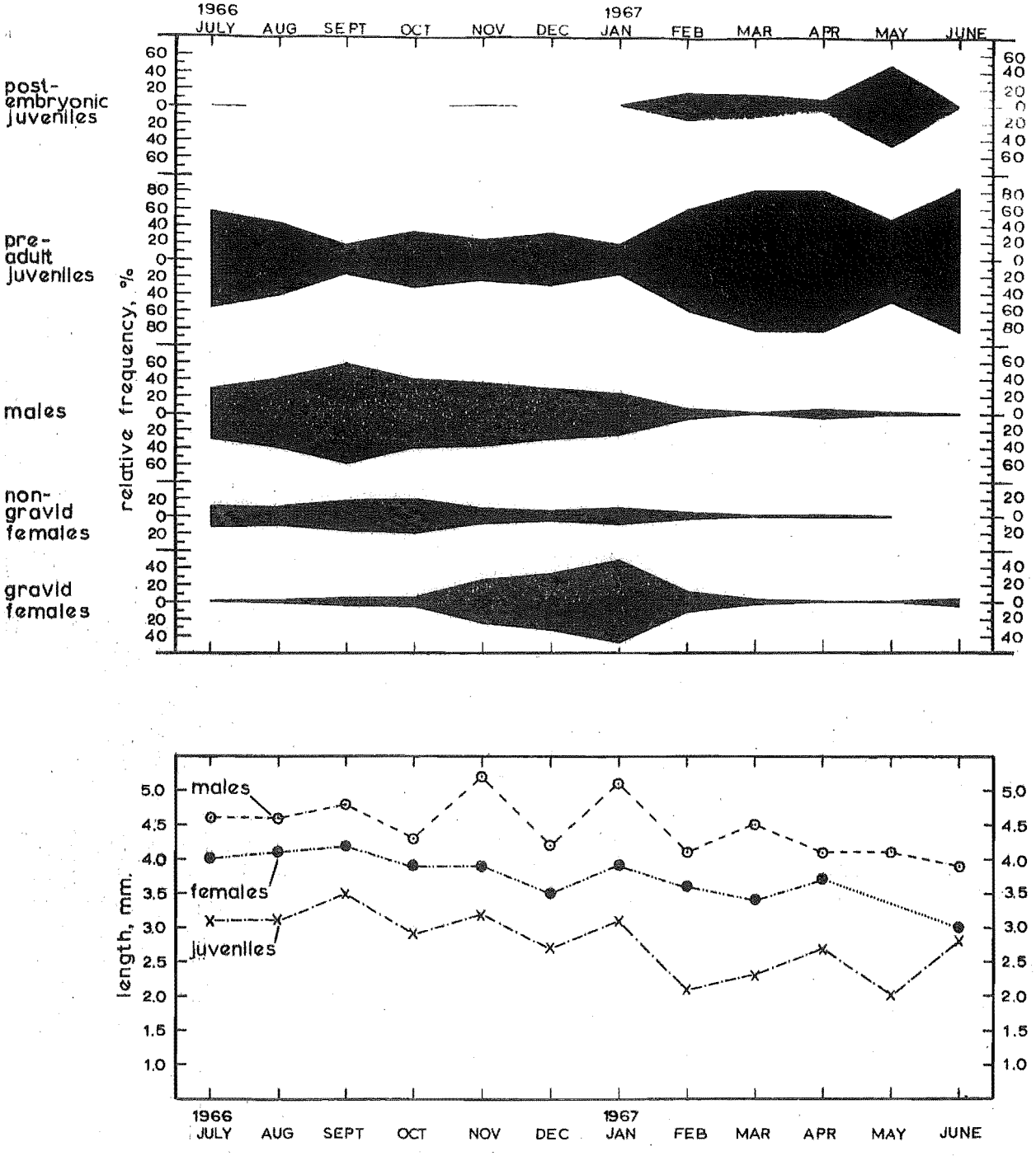
Dynamenella cordiforaminalis

Figure 34

Percentage frequency of Dynamenella cordiforaminalis in each size class (0.5 mm), in monthly samples taken from July 1966 to June 1967 at Sugarload Rocks, Kaikoura (class II and III shores).

Figure 35

Mean lengths and SDs of samples of D. cordiforaminalis taken as in Fig. 34.



Dynamenella cordiforaminalis

Figure 36

Changes in the breeding structure of a population of Dynamenella cordiforaminalis, from monthly samples taken as in Fig. 34.

Figure 37

Mean lengths of juveniles, males and females of D. cordiforaminalis, from samples taken as in Fig. 34.

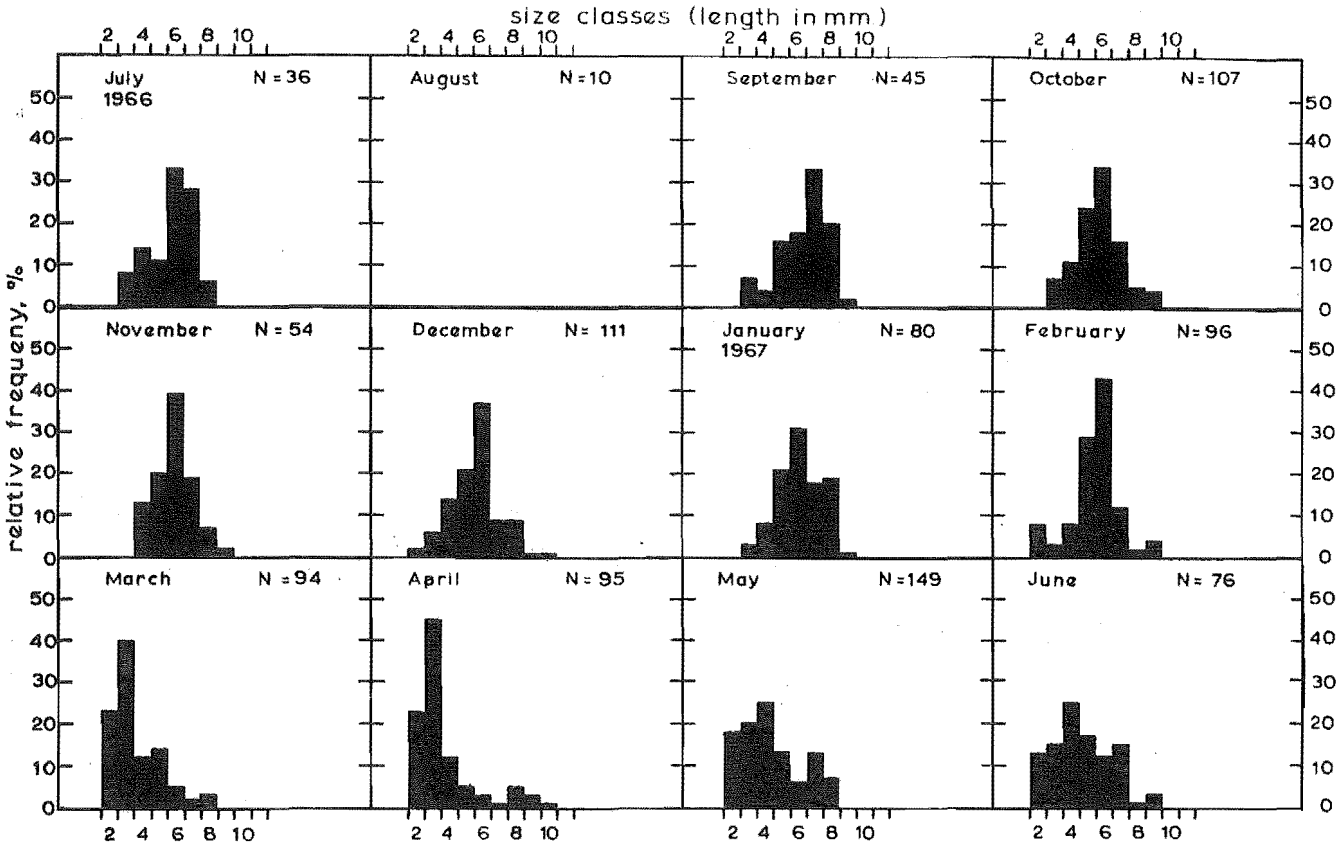
b. Algal-cryptic species

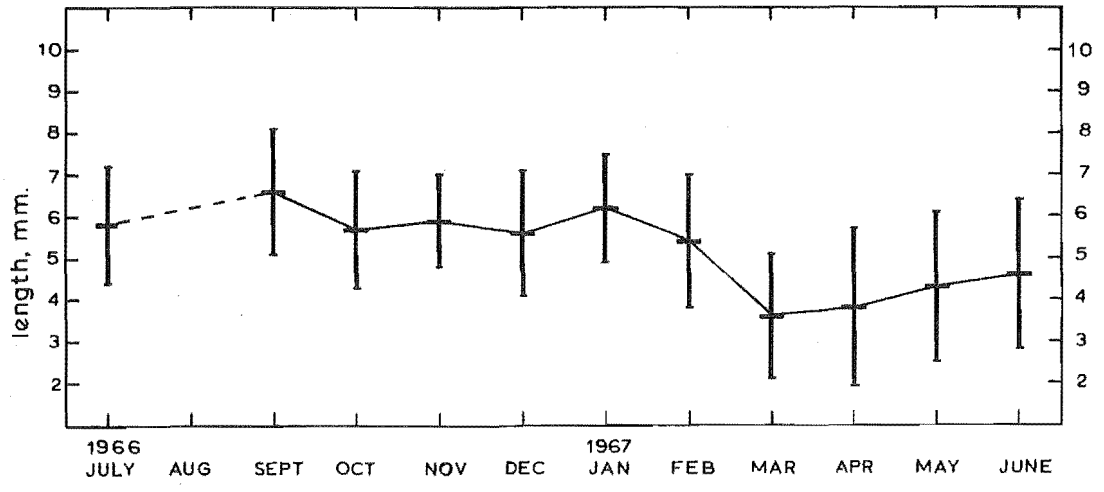
1. Dynamenella cordiforaminalis

Monthly samples of D. cordiforaminalis were collected from a class II shore (Sugarloaf Point). Small numbers of post-embryonic juveniles (1.5 mm) appeared irregularly in the samples from July to January, increasing from February to March following a large increase in the numbers of gravid females from October to January (Figs 34 and 36). Sample mean lengths (Fig. 35) fluctuated between 3.5 and 4.5 mm from July to January, falling with the increase in post-embryonic juveniles in February; at the same time the mean lengths of males and females fell (Fig. 37) as the proportions diminished (Fig. 36), indicating death of the larger adults after breeding.

Protracted breeding with a marked peak in the summer from November to January is indicated by the progression of development: from pre-adult juveniles in July and August to males and non-gravid females in September and October, followed by the increase in gravid females from November and the simultaneous decrease in males and non-gravid females.

Again, heavy juvenile mortality is suggested by the relatively high proportion of gravid females (up to 50% in January) together with the low proportion of post-embryonic juveniles (50% in May).





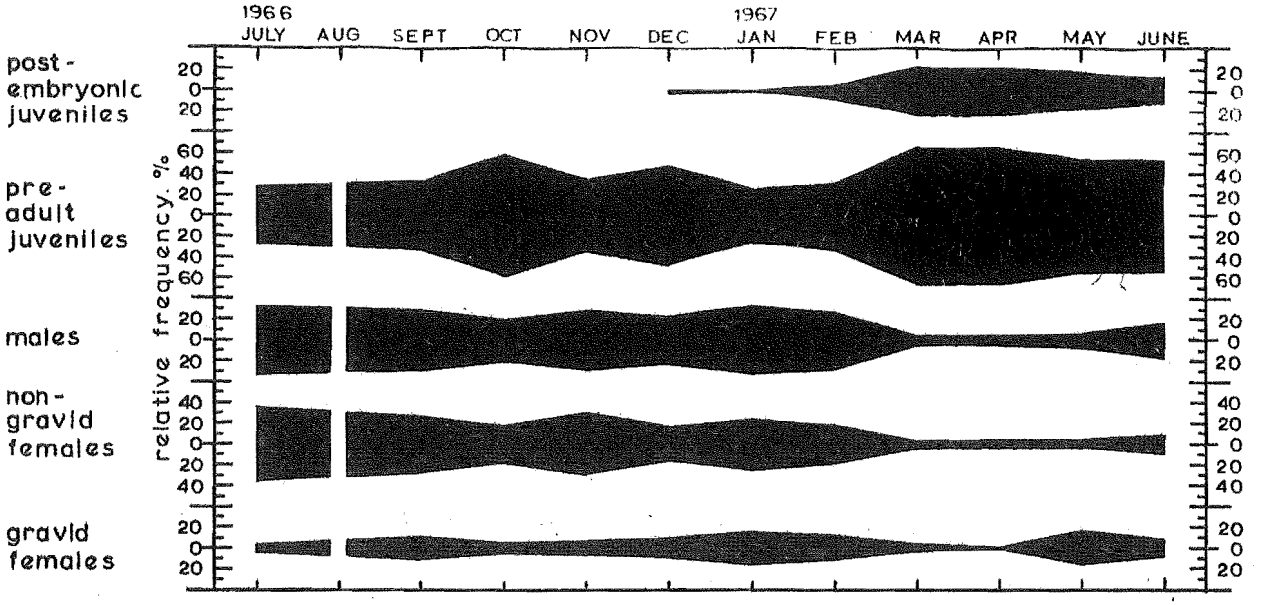
Dynamenopsis varicolor

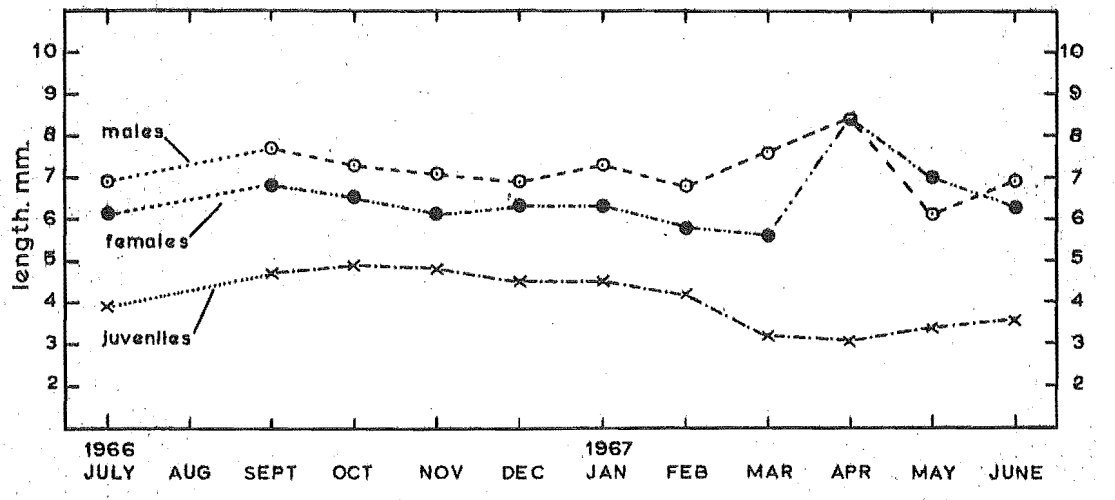
Figure 38

Percentage frequency of Dynamenopsis varicolor in each size class (1 mm), from monthly samples taken from July 1966 to June 1967 at Sugarloaf Rocks, Kaikoura (class II shores).

Figure 39

Mean lengths and SDs of samples of D. varicolor taken as in Fig. 38.





Dynamenopsis varicolor

Figure 40

Changes in the breeding structure of a population of Dynamenopsis varicolor, from monthly samples taken as in Fig. 38.

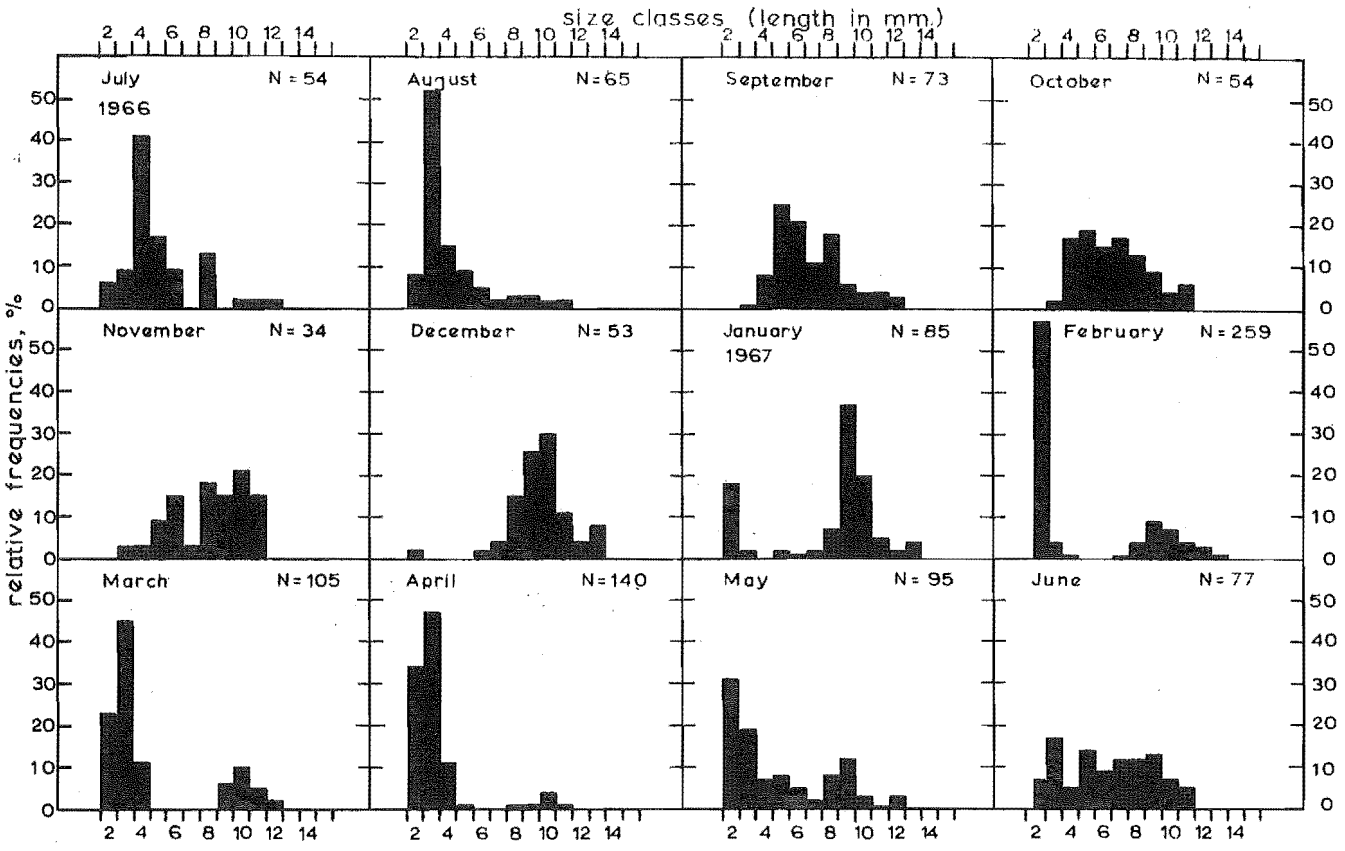
Figure 41

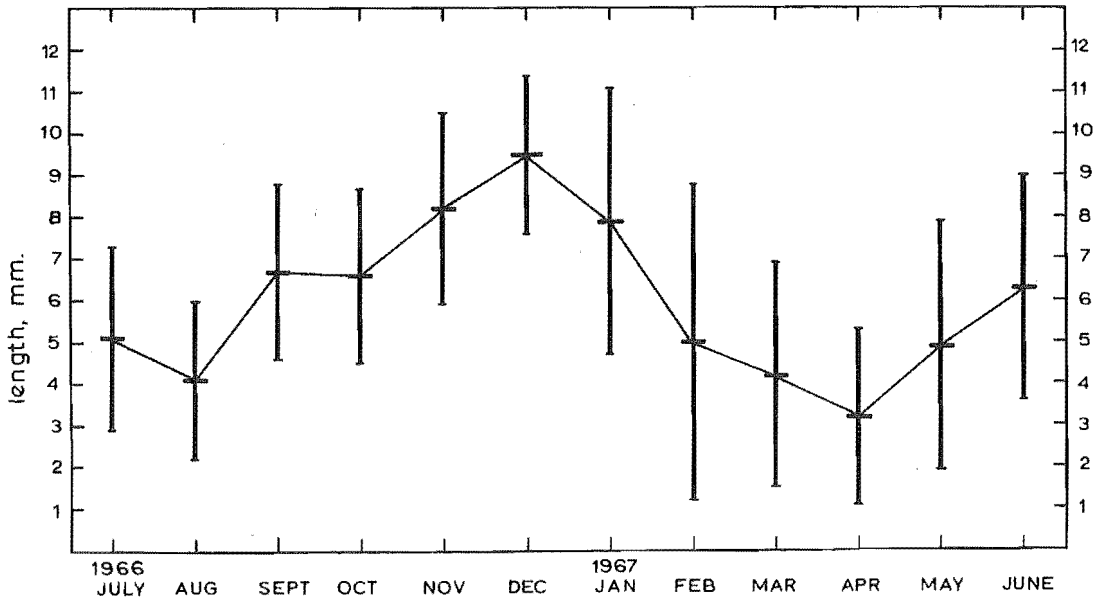
Mean lengths of juveniles, males and females of Dynamenopsis varicolor, from samples taken as in Fig. 38.

2. Dynamenopsis varicolor

Monthly samples of D. varicolor were collected on a class II shore (Sugarloaf Point). The samples from July to January comprised pre-adult juveniles and adults, size ranges and sample mean lengths remaining fairly constant (Figs 38, 39). Although gravid females were present throughout the year, post-embryonic juveniles did not appear before December, increasing considerably from February to March, then declining slightly but regularly to June (Fig. 40). In February and March, the proportions of adults decreased, the sample mean lengths and numbers of larger adults ($\geq$ 6 mm) reaching minimum values in March, indicating death after breeding (Figs 38, 39). Increasing sample mean lengths (Fig. 39) and proportions of adults (Fig. 40) indicated growth and development during April, May and June.

From the presence of gravid females in relatively constant proportions in all samples, breeding appears to be continuous; the absence of post-embryonic juveniles from July to November is probably due to increased mortality rather than to decreased breeding.





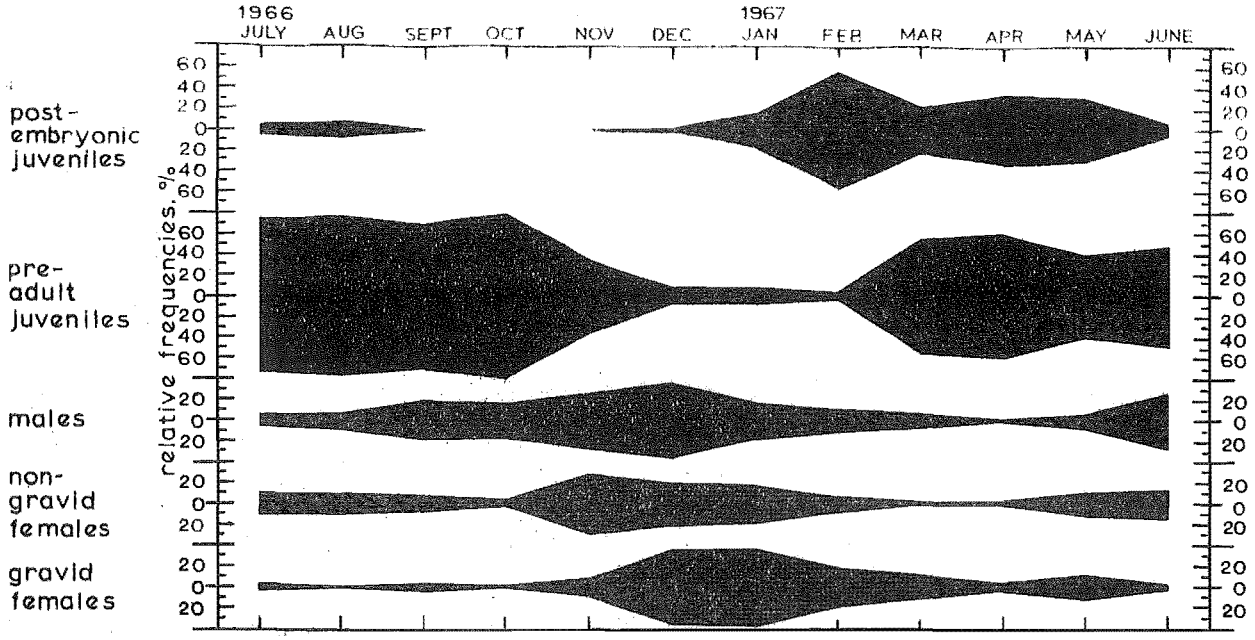
Dynamenella huttoni

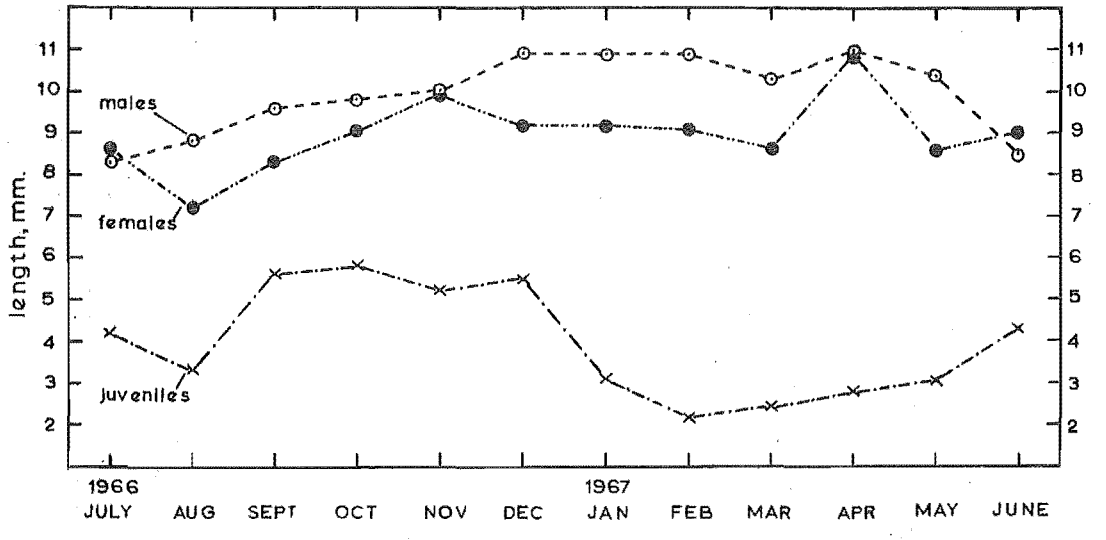
Figure 42

Percentage frequency of Dynamenella huttoni in each size class (1 mm), from monthly samples taken from July 1966 to June 1967 at Seal Reef, Kaikoura (shore classes I and II).

Figure 43

Mean lengths and SDs of samples of D. huttoni taken as in Fig. 42.





Dynamenella huttoni

Figure 44

Changes in the breeding structure of a population of Dynamenella nuttoni, from monthly samples taken as in Fig. 42.

Figure 45

Mean lengths of juveniles, males, and females of Dynamenella huttoni, from samples taken as in Fig. 42.

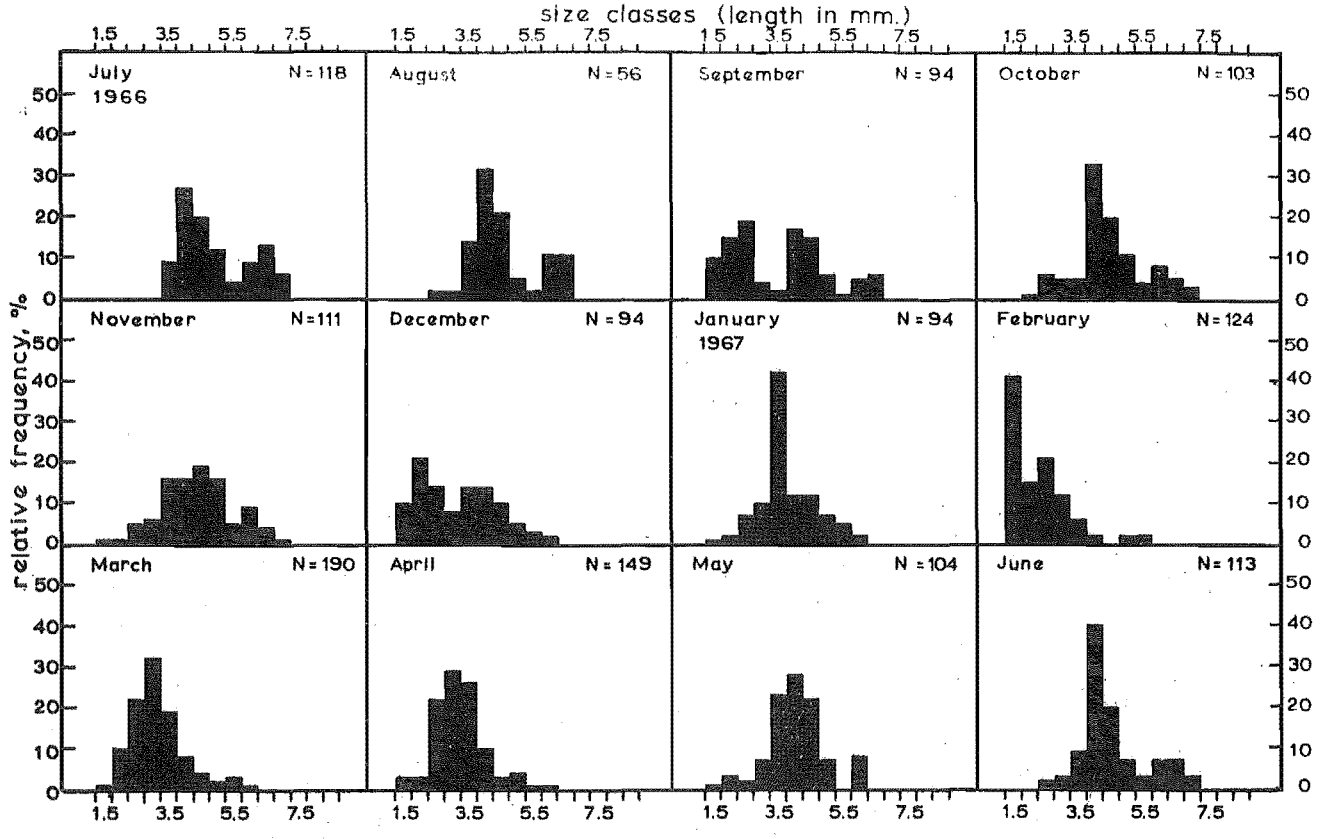
3. Dynamenella huttoni

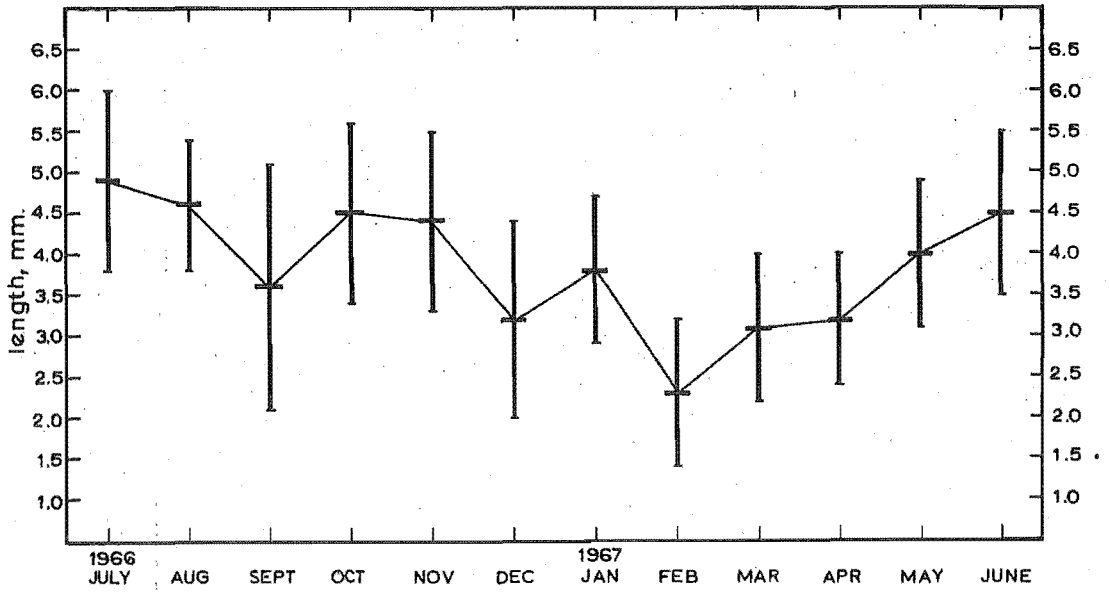
Monthly samples of D. huttoni were taken on a class I shore (Seal Reef). From July to October the samples largely comprised pre-adult juveniles (3 - 6 mm), with small numbers of post-embryonic juveniles (< 3 mm) and adults (> 6 mm) including gravid females (Figs 27, 29). From November to February proportions of pre-adult juveniles decreased as those of adults increased, preceding the increase in post-embryonic juveniles in February and the following months. Numbers of adults decreased after the January breeding peak, as post-embryonic juveniles grew into the pre-adult classes. The continuous presence of gravid females and of post-embryonic juveniles except in October again indicated continuous breeding with a summer peak indicated by increased numbers of gravid females in December and January, and of post-embryonic juveniles in February.

Sample mean lengths (Fig. 43) increased steadily indicating growth from August to December but decreased to April with the appearance of numerous young and disappearance of the large breeding adults, rising again with growth to June. Although mean lengths of juveniles (Fig. 45) followed the same trend as sample mean lengths (Fig. 43), those of males and females (Fig. 45) rose to December but did not fall appreciably until March, following the peak in

breeding in January. This appears to confirm the suggestion (p.38) that the juveniles displaced to Corallina officinalis tend to die off before breeding, since if significant numbers returned to mature with those already among the holdfasts, the mean lengths of adults would be expected to fall before or during the peak breeding season. The population thus appears to be maintained by the relatively small numbers remaining in the exposed holdfasts of Durvillea antarctica and Carpophyllum maschalocarpum.

The majority of young appear in the late summer and autumn (February to May), grow through the winter and develop and then breed in the spring and early summer (September to December), producing young and dying off in the late summer and autumn.





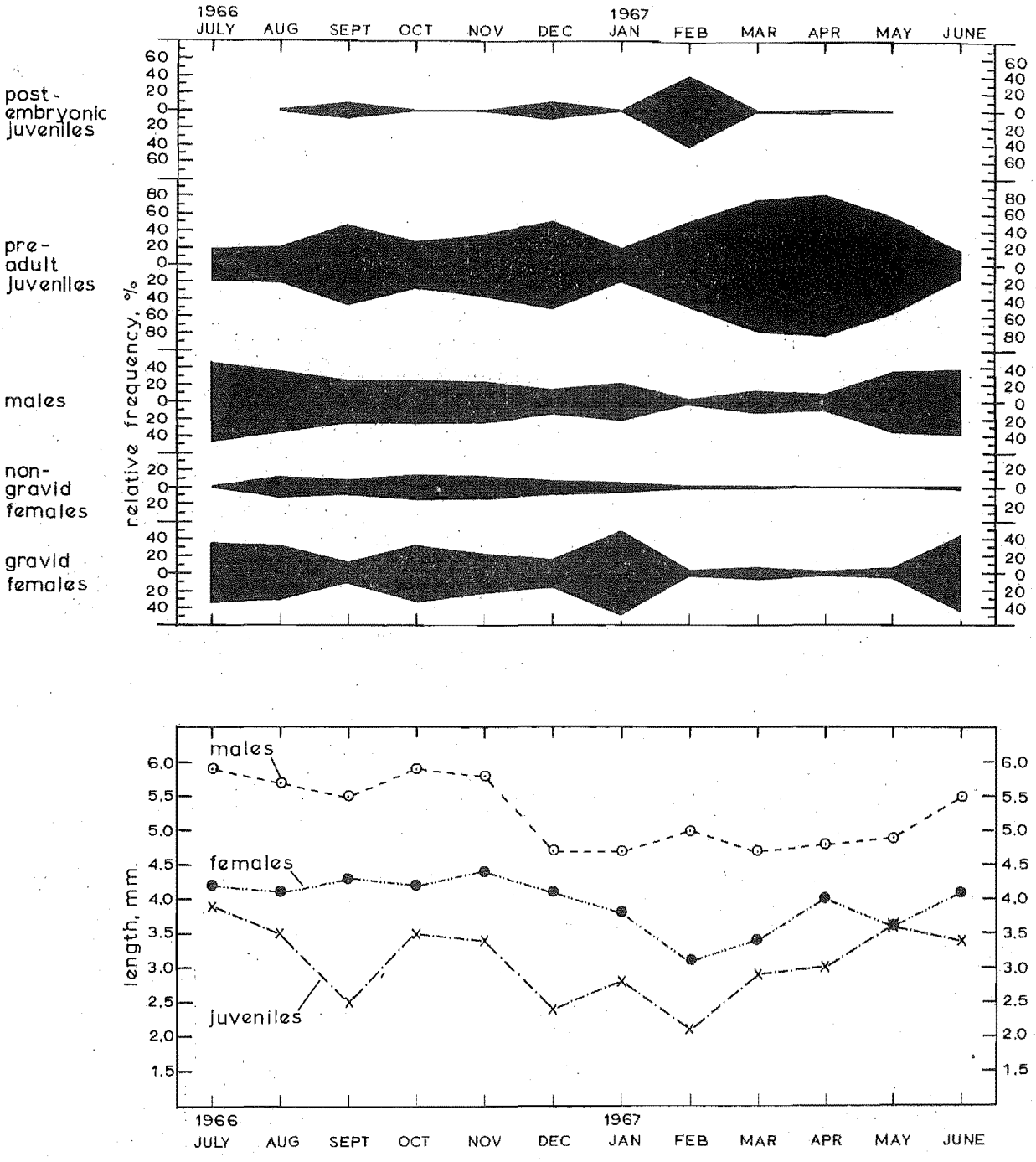
Scutuloidea maculata

Figure 46

Percentage frequency of Scutuloidea maculata in each size class (0.5 mm), from monthly samples taken from July 1966 to June 1967 at Sugarloaf Rocks, Kaikoura (class II shore).

Figure 47

Mean lengths and SDs of samples of S. maculata taken as in Fig. 46.



Scutuloidea maculata

Figure 48

Changes in the breeding structure of a population of Scutuloidea maculata, from monthly samples taken as in Fig. 46.

Figure 49

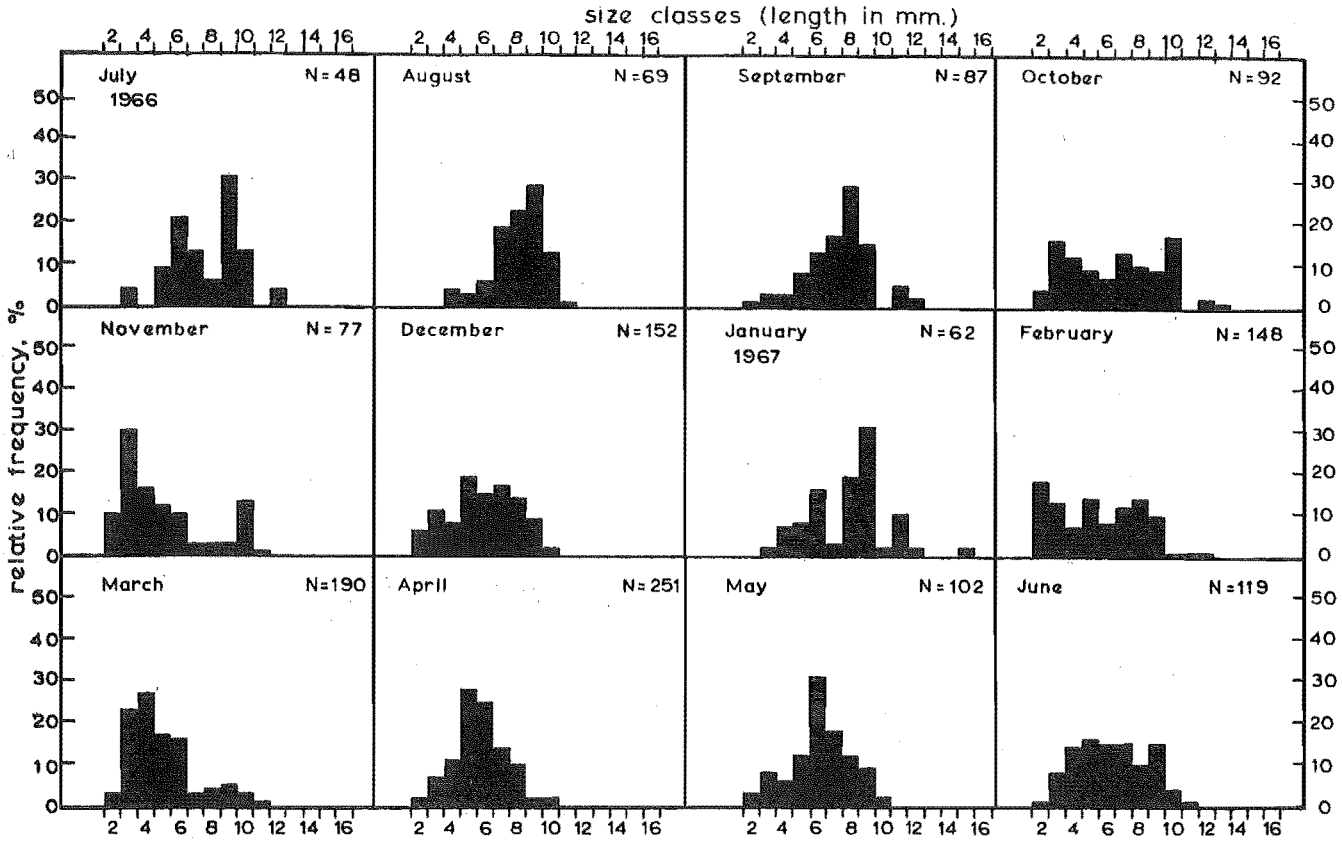
Mean lengths of juveniles, males, and females of Scutuloidea maculata, from samples taken as in Fig. 46.

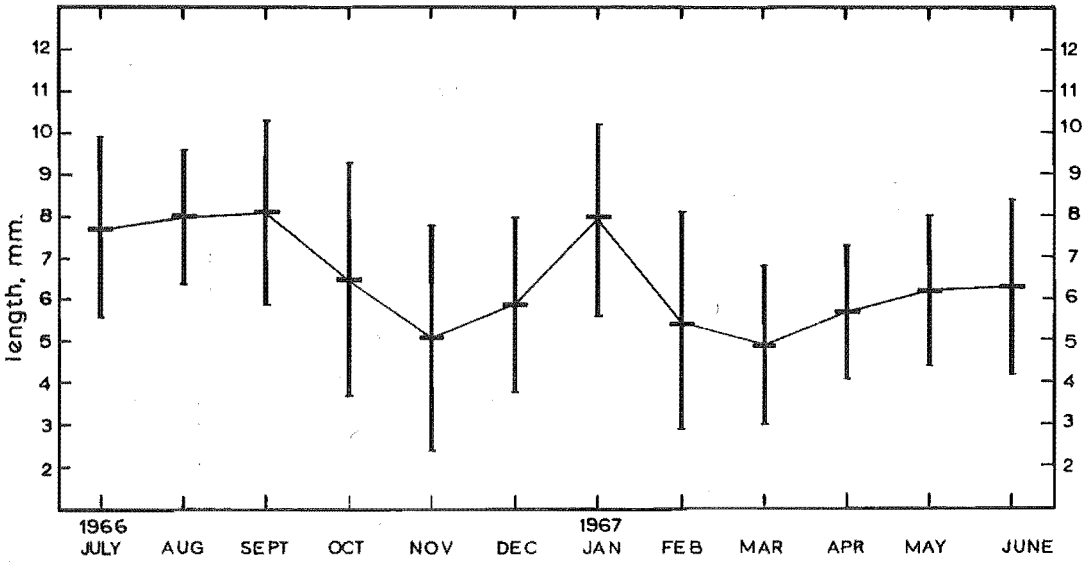
c. Species living on algal fronds

1. Scutuloidea maculata

Monthly samples were taken on a class II shore (Sugarloaf Point). Sample mean lengths (Fig. 47) fell irregularly from July to February, dips in the curve corresponding with increases in numbers of post-embryonic juveniles (Fig. 48). At the same time the mean lengths of males and females (Fig. 49) fell; in late summer, 3.0 mm females were often gravid, but in winter were still pre-adult. Frequencies of the larger classes (>5.5 mm) (Fig. 46) and mean lengths of males and females (Fig. 49) were low after December, indicating death of the larger individuals after breeding. Mean lengths of males and females and sample mean lengths increased from February, indicating a period of growth and development, males and females rising from May and June.

The small numbers of post-embryonic juveniles relative to the proportions of gravid females suggest a high rate of juvenile mortality. The peak in post-embryonic juveniles in February may thus be due to reduced juvenile mortality rather than to increased breeding activity.





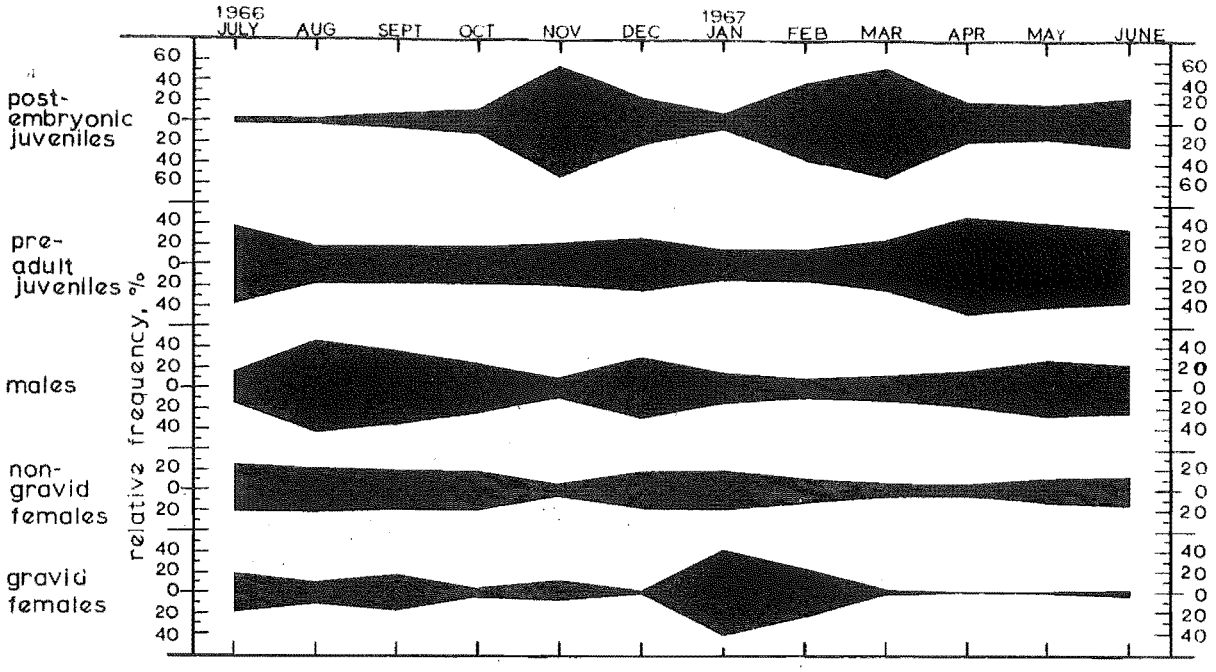
Amphoroidea falcifer

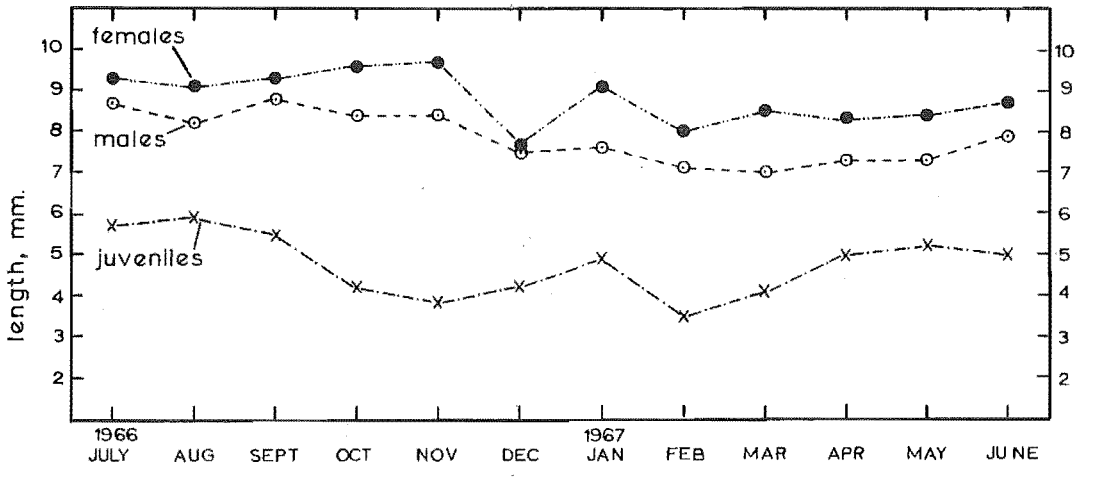
Figure 50

Percentage frequency of Amphoroidea falcifer in each size class (1 mm), from monthly samples taken from July 1966 to June 1967 at Sugarloaf Rocks, Kaikoura (class II shore).

Figure 51

Mean lengths and SDs of samples of A. falcifer taken as in Fig. 50.





Amphoroidea falcifer

Figure 52

Changes in the breeding structure of a population of Amphoroidea falcifer, from monthly samples taken as in Fig. 50.

Figure 53

Mean lengths of juveniles, males, and females of A. falcifer, from samples taken as in Fig. 50.

2. Amphoroidea falcifer

Monthly samples were taken on a class II shore (Sugarloaf Point). Males and gravid females were present throughout the year, the latter increasing slightly in July and September, greatly in January, preceding the increases in post-embryonic juveniles (Fig. 52). Mean lengths of males and females (Fig. 53) fell from September to March indicating development of pre-adult juveniles; lower maximum lengths from March suggested death of the largest males and females after breeding (Fig. 50). Post-embryonic juveniles were present in all the samples (Fig. 52), in large numbers in November and in February and March. The reduction in post-embryonic juveniles in December and January appears to be due to increased mortality rather than to declining breeding activity. The steadily increasing sample mean lengths (Fig. 51) from March to June indicated growth of the young produced in February and March.

Again continuous breeding is apparent with a protracted summer increase in breeding activity extending from November to March.

Discussion

All sizes and developmental (including embryonic) stages were effectively present throughout the year in all species, the generations overlapping completely as in some insect populations (Davidson 1944). Variation occurred in the growth rate of individuals released and reared in the laboratory. It was therefore not possible to follow growth and development in one generation.

In Sphaeromidae as in all isopods, development is direct and 'internal', in brood sacs, so that no recruitment from planktonic larvae takes place. Each species population must therefore maintain itself from its own reproductive capacity. Differences in adult and juvenile distribution and the lack of correspondence between proportions of gravid females and post-embryonic juveniles suggest that juvenile mortality is heavier in species exposed to heavier wave action. Increased reproductive capacity would therefore be advantageous in these species.

Reproductive capacity is influenced by a number of factors, including numbers of broods per female, number of young per female, sex ratio (here estimated as the proportion of females in the total numbers of males and females in monthly samples), length of breeding season.

In each species, the majority of females were assumed to produce one brood (see also Kinne, 1954; Jensen, 1955; Naylor, 1955b). Gravid females in each species occurred in a range of size classes, but the majority were concentrated in one class, the numbers in larger and smaller classes falling rapidly. If females produced more than one brood a more even size distribution would be expected.

Numbers of young per female in Sphaeromidae are limited by the size of the females, and because of the internal development, by the size of the final embryonic stage (Table 16). Numbers of young per female were estimated as the numbers of embryos in the brood sacs of gravid females in the dominant size class (Table 16).

Sex ratios were calculated as the proportions of females in the total adults in the monthly samples (Table 15). In the species living among stones the proportion of females is low in Isocladus armatus, intermediate in Exosphaeroma obtusa, high in Isocladus magellanicus and very high in Cymodocella tubicauda (relative to a hypothetical proportion of 0.5). In the algal-cryptic species, the proportion of females is lower in Dynamenella cordiforaminalis and Dynamenopsis varicolor, higher in Dynamenella huttoni. In Scutuloidea maculata and Amphoroidea falcifer, living on algal fronds, the proportions of females do not differ significantly. There is

thus a tendency for the proportions of females to increase in the more exposed species in each ecological group, relatively more in the smaller species (C. tubicauda, D. cordiforaminalis).

The percentage of gravid females in the whole population is a function of the rate of development and of the sex ratio, and varied considerably with exposure to wave action, again increasing more in the smaller species (Table 17).

Reproductive capacities were calculated for each species as the product of the numbers of young per female and the average percentage of gravid females in the monthly samples. Within each of the ecological groups reproductive capacities increased with exposure to wave action (Table 17). The average percentages of post-embryonic juveniles (Table 17) on the other hand tended to fall with increased exposure, in spite of the rise in reproductive capacities.

Continuous breeding in all species was indicated by the presence throughout the year of gravid females with embryos in all stages of development, or post-embryonic juveniles, or both. Continuous or prolonged breeding in isopods has been reported also in Sphaeroma hookeri (Kinne, 1954; Jensen, 1955), Idotea emarginata (Naylor, 1955b), and in Glyptonotus antarcticus (Dearborn, 1967). Continuous breeding is clearly advantageous in species with relatively

low fecundity and high juvenile mortality as otherwise progressive decimation may reduce numbers and opportunities for mating below levels adequate to maintain the population.

All evidence thus supports the hypothesis that reproductive capacities are increased in rocky shore species exposed to heavier wave action as a compensation for higher juvenile mortality.

Table 15. Sex ratios in rocky shore Sphaeromidae: a. species living among stones; b. algal-cryptic species; c. algal-frond species.

	N	f	p.f.	95% confidence intervals
a.				
I. armatus	681	293	0.430	0.393 - 0.467
E. obtusa	607	325	0.535	0.496 - 0.574
I. magellanicus	847	458	0.541	0.507 - 0.575
C. tubicauda	588	417	0.709	0.671 - 0.747
b.				
D. cordiforaminalis	494	221	0.447	0.403 - 0.491
D. varicolor	459	200	0.436	0.390 - 0.482
D. huttoni	466	281	0.603	0.557 - 0.649
c.				
S. maculata	658	343	0.521	0.483 - 0.559
A. falcifer	596	299	0.502	0.461 - 0.543

Legend: N, total numbers of females and males; f, total numbers of females; p.f., proportions of females.

Table 16. Fecundity and larval size in rocky shore Sphaeromidae: a. species living among stones; b. algal-cryptic species; c. algal-frond species.

	gravid females length, mm		young per female		embryos length, mm
	range	mode	range	mode	
a.					
I. armatus	5 - 9	7	48-102	81	1.6
E. obtusa	8 -12	10	47-114	77	1.6
I. magellanicus	5 - 9	6	12- 82	54	1.8
C. tubicauda	3.0 - 5.0	3.5	12- 15	14	1.4
b.					
D. cordiforaminalis	3.0 - 4.5	4.0	16- 38	31	1.5
D. varicolor	6 - 9	7	42-136	78	1.8
D. huttoni	7 -10	9	66-168	112	1.7
c.					
S. maculata	3.5 - 5.0	4.0	22- 73	42	1.1
A. falcifer	7 -12	9	52- 90	74	2.2

Table 17. Reproductive capacities, percentages of gravid females and post-embryonic juveniles in rocky shore Sphaeromidae: a. species living among stones; b. algal-cryptic species; c. algal-frond species.

	gravid females, %	reproductive capacity	post-embryonic juveniles, %
a.			
I. armatus	0.5	40.5	15.7
E. obtusa	8.0	616.0	12.5
I. magellanicus	21.7	1171.8	6.1
C. tubicauda	44.7	625.8	10.0
b.			
D. cordiforaminalis	11.6	359.6	7.4
D. varicolor	8.2	639.6	7.3
D. huttoni	11.6	1299.2	15.3
c.			
S. maculata	22.1	928.2	5.5
A. falcifer	11.3	836.2	23.9

DISCUSSION

The evidence suggests that ecological distribution of littoral species of Sphaeromidae can be explained by the combined interactions of the biological factors examined, external morphology, physiological tolerances, and breeding, with the environmental conditions of wave action and substrate, periods of emergence and fresh water influence.

In the rocky shore species, ecological groups are recognisable on the basis of predominance on different types of substrate: stones, shrubby and crustose algae and algal holdfasts, and flat algal fronds. The brackish water species also appear to be similarly segregated by substrate. Species in each substrate-group are characterised by a number of common morphological characters which distinguish them from the species of other groups. Thus the pereopods and claws of the algal-cryptic and algal-frond species are stouter (or longer as in Scutuloidea maculata) than those of the species living among stones. But the bodies of the algal-cryptic species are deeper in cross-section, with rugose or tubercular surfaces, whereas those of the algal-frond species are dorso-ventrally flattened, with smooth surfaces; the bodies of the species living among stones are intermediate in both cross-section

and surface sculpture (except in Cymodocella tubicauda, a very small species in which the profile is deep). Similar differences exist also in the brackish water species: in Sphaeroma quoyana, living in burrows, the body section is deep and the surface smooth; in Pseudosphaeroma campbellensis, living under stones, the body is dorso-ventrally flattened, the surface smooth; in Paradynamenopsis crenellata, living among Mytilus, comparable with the algal-cryptic substrate, the cross-section is deep, the surface rugose and tubercular.

Morphological differences are also related to the degree of wave action to which each species is typically exposed. In each group, the body is more robust, and the pereopods and claws stouter in the species exposed to heavier wave action.

Differences in external morphology accordingly indicate adaptive specialisations which extend the ecological range of the family as a whole, but limit the distribution of individual species. Thus the distribution and relative abundance of each species is limited by the extent or absence of the appropriate substrate, and of the less robust species by their reduced ability to withstand damage and displacement by wave action. While a more robust body and stouter appendages do not appear to be disadvantageous in less exposed conditions, the species so equipped are limited by their physiological tolerances.

Physiologically, species tolerances vary directly with the range of conditions which obtain at different levels and on different classes of shore. The species of lower levels and more exposed shores are less tolerant of higher temperatures, of higher and lower than normal salinities, and of exposure to air, than species of higher levels and more sheltered shores, including brackish water situations, and are accordingly limited in their distribution. Differences in the distributions of adults and juveniles however, especially in the algal-cryptic species, indicate that considerable proportions of juveniles are exposed to conditions which are probably lethal.

The differences in the adult and juvenile distributions together with the considerable overlapping among the rocky shore species are taken to indicate that many individuals are displaced by wave action from the proper specific habitat-niches, which are considered to be where the main centres of concentration of the breeding adults are located. This view appears to agree with that regarding Idotea, expressed by Naylor (1955a) 'Idotea occur mostly amongst algae and, since shore algae may be washed away from the intertidal zone and sublittoral algae may be washed ashore, some mixing of sublittoral and littoral Idotea must take place. Wherever possible, therefore,

extended observations must be made on resident breeding populations, if specific environments are to be determined'.

This opinion is supported also by the large differences in reproductive capacity among the species of rocky shores. The greatly increased breeding in the species of exposed shores appears to be an adaptive response to greater juvenile mortality caused by increased displacement of juveniles by the heavier wave action.

A further question introduced by overlapping distributions and by displacement of individuals is that of behavioural adaptation. That is, to what extent selection of substrate and situation occurs versus effectively random dispersal by wave action, with survival of only those individuals which remain or chance to resettle in favourable situations. Planktonic larvae of a number of species of marine benthic invertebrates have been shown to settle preferentially or exclusively in favourable situations (Thorson, 1946; Wilson, 1951, 1952). Development in sphaeromids is direct, and both juveniles and adults in all the species studied swim actively, but all are relatively small animals, and so unable to make headway against any but the lightest wave or tidal movement.

Qualitative field and laboratory observations indicated that swimming is faster in the lighter and more flattened species, slower in the heavier species with

deeper body sections. The latter also tend to roll the body into a ball, and so to sink more rapidly. From field observations, Isocladus armatus alone of the rocky shore species swims freely on incoming tides (this behaviour was reported also in Sphaeroma rugicauda by West, 1964), and is the only species occurring typically above HWN on rocky shores (p. 24). In the laboratory, all species swam more frequently in disturbed than in still water, but less frequently when stones or pieces of seaweed were provided for settling. No preference for a particular substrate appeared when each species was offered a choice, individuals apparently settling indiscriminately on whatever was available. Direct observations were attempted by skin-diving, but were necessarily limited to calm water and clear conditions. Distributions of the species living among stones at lower levels than I. armatus were evidently the same at high and low tides. A further difference between I. armatus and the other species living among stones is that in intertidal pools, the former seem equally distributed on the upper and lower surfaces of the stones, whereas the others are confined to the lower surfaces (similar to Jaera albifrons, Sjöberg, 1967).

As stated, these observations, although repeated, were not made quantitatively. It appears however that behavioural variation also is adapted to maintaining individuals in optimal conditions, against the dispersive effect of water

movement. Thus, for example, I. armatus swim freely on incoming tides, tending to be raised to higher levels where they are physiologically adapted to survive. At the same time, this behaviour will accelerate their dispersal on more exposed shores, so reducing relative abundance. I. magellanicus on the other hand remain underneath stones on incoming tides, and if displaced, roll into a ball, sinking rapidly back to the bottom. This behaviour will reduce the displacement to higher levels, where the species is not adapted to survive. Similar patterns of behaviour presumably tend to maintain the species living among algae in favourable situations.

Juveniles newly released in the laboratory (p. 6) stayed clinging to the parent female or in the immediate vicinity for some time, further tending to concentrate the population in optimal conditions.

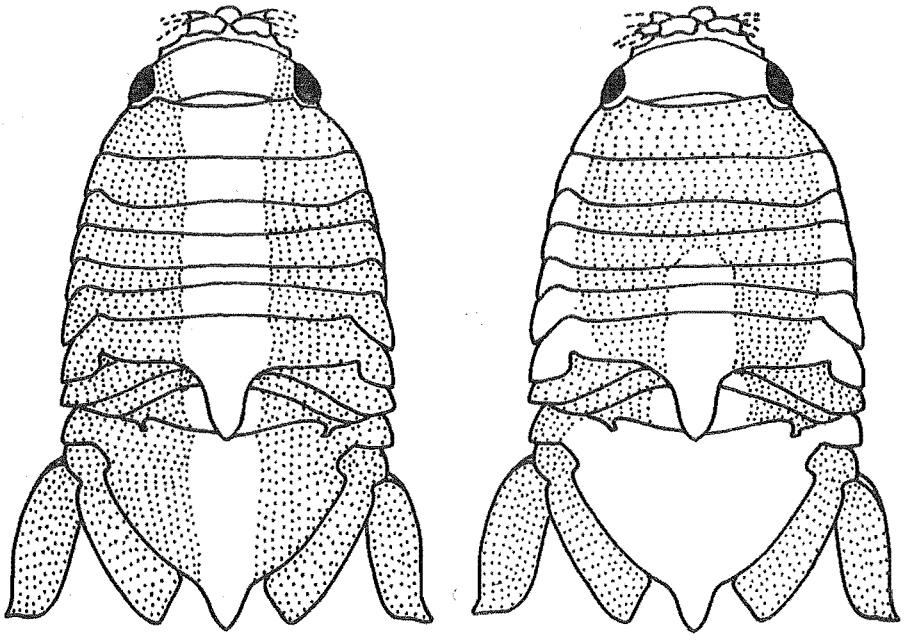
Despite the adaptive character of morphological and behavioural differences, considerable numbers in each species population are displaced, especially on exposed shores. Whether survivors among these displaced individuals can return to favourable situations during subsequent high tides in calm conditions, thus exercising selection of situation or substrate, remains an open question, which could perhaps be answered by studies providing statistically usable data.

Naylor (1955a) suggested that species of Idotea may be restricted to their particular habitat-niches and excluded from others which they could tolerate by inter-specific competition. No evidence indicating interspecific competition among littoral species of Sphaeromidae appeared in the present study. Although densities reached very high levels, up to 5000 m^{-2} in Isocladus armatus for example, the distribution within quadrats was very localised, with large areas unoccupied. Competition for space thus seems unlikely, even among species preferring the same kind of substrate. Quantitative study of food requirements and availability could perhaps indicate competition for food.

The differences in morphology, physiology, breeding, and probably behaviour, indicate however that these adaptive features are major and primary factors limiting the species distributions.

Fig. 54

Isocladus armatus: A, 'striped', B, 'variegated'; non-stippled areas show white pigment.



A B

PHENOTYPIC VARIATION IN *ISOCLADUS ARMATUS*

Colour polymorphism is common among marine invertebrates, and has been shown to be genetically determined in a number of species, including the sphaeromid isopods *Sphaeroma serratum* (Bocquet, Lévi, and Teissier, 1951) and *S. rugicauda* (West, 1964). Spatial and temporal variation in frequencies of phenotypes recognised by different colour patterns was recorded in both species. In *Sphaeroma serratum*, frequencies of the colour forms varied among allopatric populations (Bocquet *et al.*, 1951), changing temporally in some but remaining stable in others for up to 15 years (Goudeau, 1966). The inference was that the colour variation was not intrinsically adaptive, but was associated with physiological differences. Regarding *S. rugicauda*, West (1964) wrote 'The obvious correlation [in gene frequency variation] is with temperature', but 'It is obvious that temperature alone is an insufficient explanation of gene frequencies. . .'. West concluded that 'The geographical trends and changes in gene frequencies in some populations suggest that natural selection is responsible for the differences in gene frequencies between populations', but did not specify the selective factors.

In the present study, spatial and temporal variation in the frequencies of colour forms in *Isocladus armatus*, a New Zealand species of sphaeromid isopod, are examined in relation to differences between the colour forms in tolerance of temperature and salinity.

Materials and methods

1. Variation in relative frequencies of colour forms

Isocladus armatus occurs in large numbers among stones between high and low spring tide levels on fairly sheltered shores. All populations studied comprised individuals with innumerable small differences in colour and pattern, among which two distinctive forms, 'variegated' and 'striped' (Fig. 54), were consistently recognisable with 100% nonoverlap. Individuals which were neither 'variegated' nor 'striped' were lumped together as 'standard'.

Conspecificity was confirmed by isolated observations of females which released young of all the major colour patterns in the same brood. The colour patterns were retained through successive moults, and occurred in specimens of both sexes and of all sizes, and thus are not linked with sex and are not a function of age.

Random samples were collected in August and November 1966 and May 1967 from geographically separate areas (Fig. 1): Hatfield's Beach near Auckland; Wairepo Flat on the Kaikoura Peninsula; between Dunedin and Portobello in the Otago Harbour. Additional samples were collected in May, June, and July 1967 from Whaler's Bay on the Kaikoura Peninsula.

Samples were scored immediately after collecting to obviate errors from either post-mortem changes in pigmentation,

or the release of young after collecting, both of which would bias the samples.

Frequencies of 'variegated' and 'striped' were compared independently by means of χ^2 tests; each sample was considered as comprising first, 'variegated' and 'non-variegated', then 'striped' and 'non-striped'. Samples taken on two consecutive days at Whaler's Bay (June 1 and 2, Table 19) were highly homogeneous for all forms (χ^2 = 0.9, $P > 0.95$), indicating consistency in both sampling and scoring.

The frequency composition of the samples is given in Tables 18 and 19, and the percentage of each colour form in the samples is shown in Figs 55 and 56.

2. Temperature and salinity

a. Environmental conditions

Temperatures were recorded at each locality when collections were made, in pools at mid-tide level and in the shallow sublittoral water, and are given above the localities in Figs 55 and 56. Temperature and salinity were recorded at Kaikoura in the warmest and driest summer month (February), and in the coldest winter month with the greatest rainfall (July). Measurements were made during both spring and neap tides, in intertidal pools from high to low spring tide levels, and in shallow sublittoral water (Fig. 58).

b. Tolerances

Each colour form from the Kaikoura population was tested in the laboratory to compare the tolerance of temperature and salinity.

Upper lethal temperatures were determined in winter and summer by immersing 10 freshly collected specimens in sea water which was heated from room temperature (15 - 18C.) at a constant rate of 1C. per minute, with stirring to ensure uniform oxygen distribution. Results are given in Table 20.

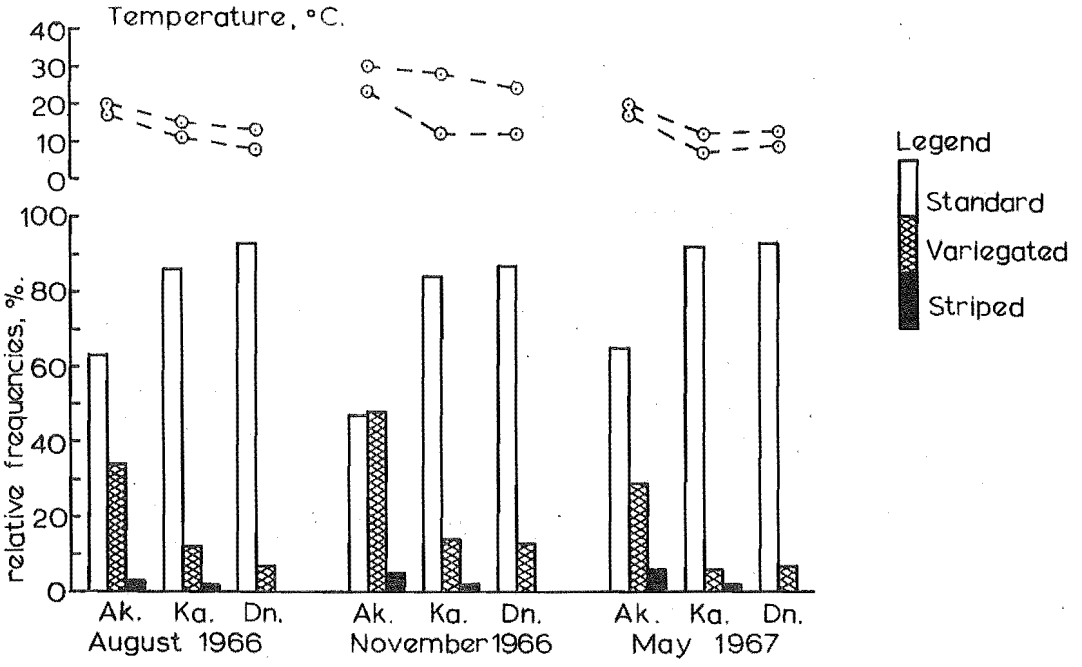
Comparison was made of salinity tolerances at 5 and 30C. Sea water ranging in salinity from 0 to 70 °/oo (0 - 200%) was prepared by diluting with distilled water, or by concentrating by evaporation. Samples of 10 freshly collected specimens of each colour form were immersed separately for 24 hours in dishes containing 500 ml of solution. Salinity was maintained constant at 30C. by regular topping up to a mark with distilled water at the same temperature. Results are shown in Fig. 57.

Table 18. Geographic and seasonal variation in frequencies of phenotypes of Isocladus armatus in New Zealand, 1966-67.

	N	'standard'	'variegated'	'striped'
August 1966				
Auckland	354	223	121	10
Kaikoura	372	320	46	6
Dunedin	210	196	14	0
November 1966				
Auckland	176	82	85	9
Kaikoura	494	419	65	10
Dunedin	64	56	8	0
May 1967				
Auckland	646	418	189	39
Kaikoura	195	180	11	4
Dunedin	536	497	39	0

Table 19. Local and temporal variation in frequencies of phenotypes of Isocladus armatus on two shores of the Kaikoura Peninsula.

		N	'standard'	'variegated'	'striped'
Wairepo Flat					
1966	June	130	121	8	1
	September	372	320	46	6
	November	494	419	65	10
1967	January	331	277	46	8
	May	116	98	16	2
	June	195	180	11	4
	July	197	182	14	1
Whaler's Bay					
1967	April 12	173	102	60	11
	May 1	182	107	66	9
	June 1	175	104	41	30
	June 2	366	232	80	54
	July 1	276	163	44	69


Temperature, °C.
40
30
20
10
0
100
80
60
40
20
0
relative frequencies, %.
Ak. Ka. Dn.
August 1966
Ak. Ka. Dn.
November 1966
Ak. Ka. Dn.
May 1967
Legend
Standard
Variegated
Striped

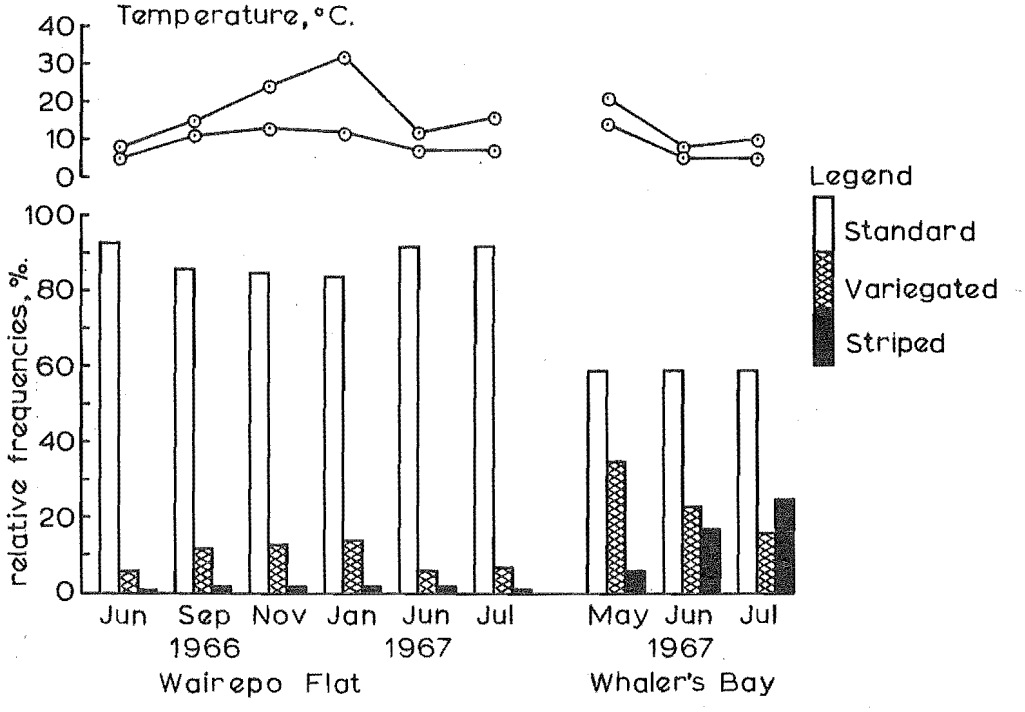
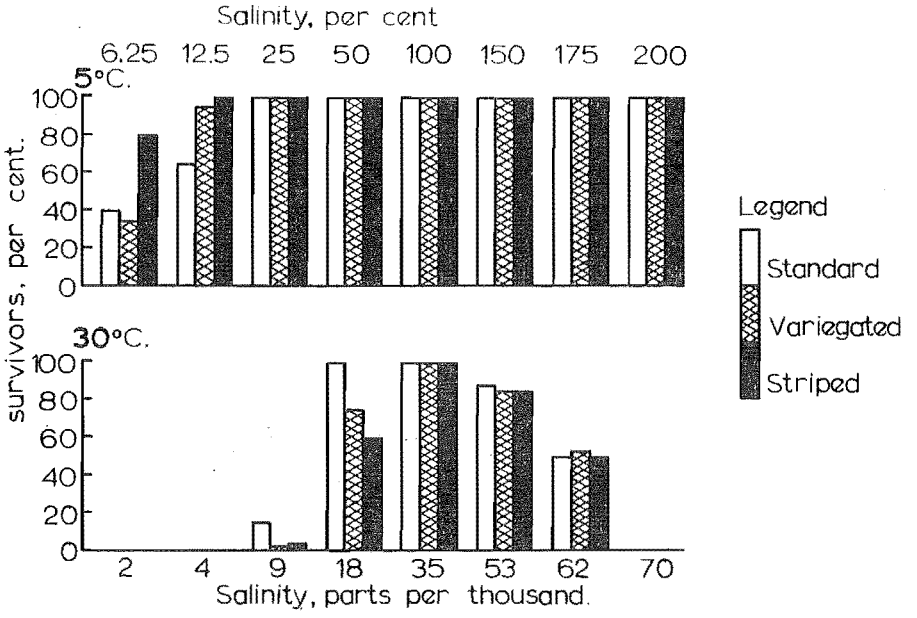

Temperature, °C.
40
30
20
10
0
100
80
60
40
20
0
relative frequencies, %.
Jun Sep Nov Jan Jun Jul
1966 1967
Wairepo Flat
May Jun Jul
1967
Whaler's Bay
Legend
Standard
Variegated
Striped

Fig. 55

Isocladus armatus: Geographical and temporal variation in proportions of colour patterns (Ak., Auckland, Hatfield's Beach; Ka., Kaikoura Peninsula, Wairepo Flat; Dn., Dunedin, Otago Harbour).

Fig. 56

I. armatus: Local and temporal variation in proportions of colour patterns on the Kaikoura Peninsula.


Salinity, per cent
6.25 12.5 25 50 100 150 175 200
5°C.
30°C.
survivors, per cent.
100 80 60 40 20 0
2 4 9 18 35 53 62 70
Salinity, parts per thousand.
Legend
Standard
Variegated
Striped

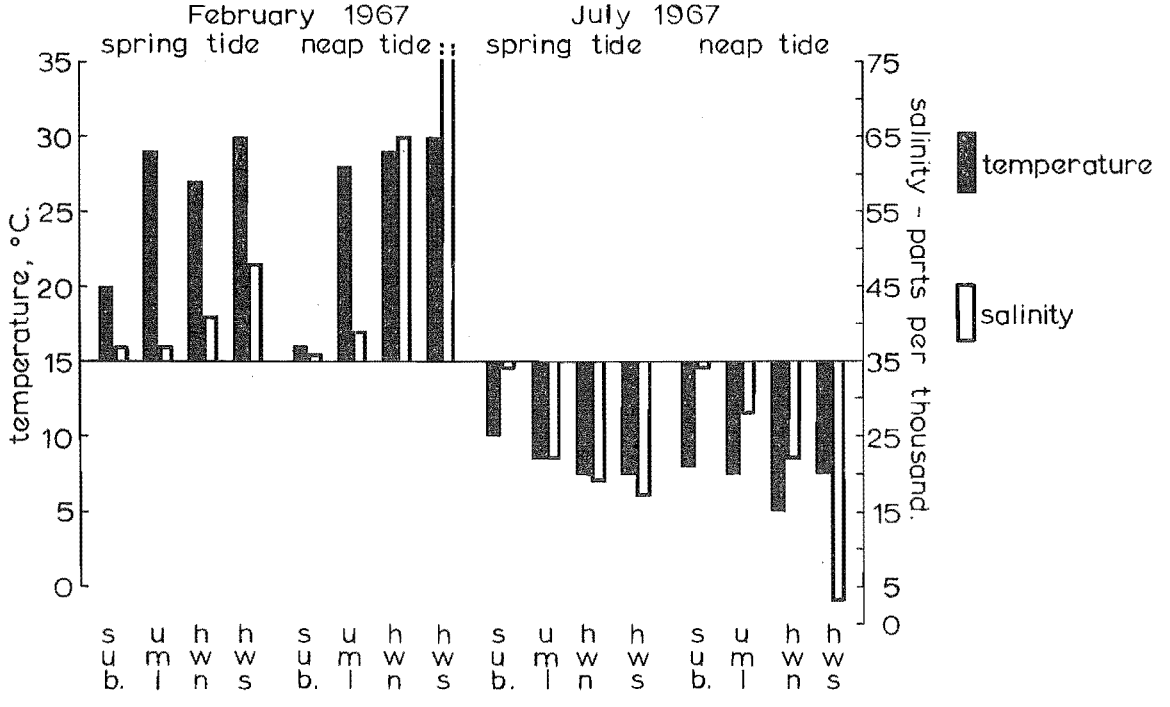

February 1967
spring tide
neap tide
July 1967
spring tide
neap tide
temperature, °C.
35 30 25 20 15 10 5 0
salinity - parts per thousand.
75 65 55 45 35 25 15 5 0
temperature
salinity
sub. ml wn ws sub. ml wn ws sub. ml wn ws sub. ml wn ws

Fig. 57

Isocladus armatus: variation in survival of colour forms in different combinations of temperature and salinity.

Fig. 58

Extreme variations in intertidal temperature and salinity on a class IV shore, Whaler's Bay, Kaikoura Peninsula. Sub = sublittoral; uml = upper mid-littoral; hwn = high water neap tide level; hws = high water spring tide level.

Table 20. Isocladus armatus: upper lethal temperatures in winter and summer of colour forms in the Kaikoura population, in degrees C.

	summer	winter
'striped'	36	33
'variegated'	39	36
'standard'	39	36

Discussion

Frequencies of 'variegated' were highest at Auckland, and lowest at Dunedin in each month except May, the differences being highly significant: in August, $\chi^2 = 82.5$, $P < 0.005$; in November, $\chi^2 = 97.6$, $P < 0.005$; in May, $\chi^2 = 120.7$, $P < 0.005$. Similarly, frequencies differed in each locality in the three months: at Auckland, $\chi^2 = 22.6$, $P < 0.005$; at Kaikoura (Wairepo Flat), $\chi^2 = 7.5$, $P < 0.025$; at Dunedin, $\chi^2 = 2.3$, $P > 0.25$. The small change in Dunedin appeared to be related to the smaller seasonal temperature difference, but overall geographic and seasonal changes correlated with temperature differences, the lowest proportion of 'variegated' always coinciding with the lowest temperatures (Table 18, Fig. 55).

At Kaikoura (Table 19, Fig. 56), on Wairepo Flat, proportions of 'variegated' again rose with temperature, from June 1966 to January 1967 ($\chi^2 = 5.2$, $P = 0.025$), falling from January to June 1967 ($\chi^2 = 8.6$, $P < 0.005$); the samples in June of both years were homogeneous for 'variegated' ($\chi^2 = 0$, $P > 0.99$). On Whaler's Bay, proportions of 'variegated' were consistently higher than on Wairepo Flat, for unknown reasons, but still fell with the temperature from May to June ($\chi^2 = 5.9$, $P < 0.025$), continuing to fall as the temperature remained low from June to July ($\chi^2 = 3.3$, $0.10 \quad P > 0.05$).

Frequencies of 'striped' were again higher at Auckland than at Kaikoura (Wairepo Flat) in each month (Table 18, Fig. 55), but the differences were of doubtful significance: in August, $\chi^2 = 1.0$, $P > 0.25$; in November, $\chi^2 = 3.3$, $0.10 > P > 0.05$; in May, $\chi^2 = 3.6$, $0.10 > P > 0.05$. No 'striped' occurred in Dunedin samples. In the Auckland samples, frequencies differed significantly in the three months ($\chi^2 = 10.4$, $P = 0.005$), again rising and falling with temperature. Considerable differences however appeared between the two Kaikoura shores (Table 19, Fig. 56). On Wairepo Flat, the samples were homogeneous for 'striped' ($\chi^2 = 0.2$, $P > 0.95$), whereas on Whaler's Bay, 'striped' rose sharply as the temperature fell from May to June ($\chi^2 = 14.1$, $P < 0.005$), continuing to rise as temperatures remained low from June to July ($\chi^2 = 10.5$, $P < 0.005$).

Upper lethal temperatures in 'striped' were lower than in 'variegated' and 'standard' in both summer and winter (Table 20), but a higher percentage of 'striped' (80%) than 'variegated' (38%) and 'standard' (40%) survived after 24 hours immersion at 5C. in a salinity of $2^{o}/oo$ (Fig. 57). These results are consistent with the geographic and seasonal differences in proportions of 'variegated'. They do not however appear to be consistent with the higher proportion of 'striped' in the warmer Auckland area, or with the absence of this form from the cooler Dunedin area; nor do they account for the large

differences in proportions of 'variegated' between Wairepo Flat and Whaler's Bay (Kaikoura).

The anomalous distribution of 'striped' may however be explained by a further correlation. Fig. 55 shows that the higher proportions of 'striped' coincide with higher proportions of 'variegated', being consistently higher at Auckland than at Kaikoura (Wairepo Flat). In Auckland, the proportions of both rose with temperature from August to November, the lower temperature tolerance limiting the increase in 'striped'. Between November and May the proportions fell in 'variegated' but rose in 'striped', corresponding with the drop in temperature. Similarly, at Whaler's Bay (Fig. 56), the proportions fell in 'variegated' but rose in 'striped', as the temperature dropped from May to July.

A number of genetic combinations and interactions could produce this situation, among which the simplest might be that 'variegated' were heterozygous for a recessive allele for which 'striped' were homozygous. In populations in which 'variegated' were present in low frequencies, say 0.10, the frequency of the recessive allele would then be 0.05, and of the recessive homozygote 0.0025. Thus the absence of 'striped' from the Dunedin population might be more apparent than real. Controlled breeding in the laboratory would however be necessary to investigate this aspect.

Other factors such as direct adaptive value of coloration (concealment from predators), non-random mating, differential fecundity, cannot, without evidence, be excluded from contributing to differences in the relative frequencies of colour forms. The field and laboratory data are however consistent with the hypothesis that colour patterns in Isocladus armatus are associated with physiological differences, and that the geographic variations and seasonal changes in local populations are, at least in part, produced by the selective effects of temperature and salinity.

Dobzhansky (1951, p.110) wrote 'A single genotype, no matter how versatile, could hardly function with maximal efficiency in all environments. Hence, natural selection has preserved a variety of genotypes, more or less specialized to render the organism efficient in a certain range of the existing environments.'

In Isocladus armatus, the biological significance of the phenotypic variation appears to be that the range of tolerance of shore conditions is extended, to the advantage of the species and the local populations, at the cost of the lives of many individuals with a phenotype which is less adaptive in a particular locality and in a particular season. Thus in Auckland, 'striped' are less successful because of the higher temperatures, but on

Whaler's Bay at Kaikoura, 'striped' are more successful because of the lower winter temperatures, and contribute to the fitness of the winter population which is maintained at a higher level than would otherwise be possible.

ACKNOWLEDGEMENTS

I should like to thank Professor G.A. Knox and Dr R.S. Bigelow for their encouraging supervision of this thesis, and Dr D.E. Hurley for indispensable taxonomic help. I am grateful to technical help and provision of equipment by Mr R.H. Thompson (Technical Officer) and Mr J.T. Kay (Stores Officer) and Mr J.T. Darby (Photographer). Lastly I acknowledge my indebtedness to the New Zealand University Grants Committee for the award of a New Zealand Post-Graduate Scholarship which made it possible to carry out this work.

REFERENCES

BALLANTINE, W.J. 1961: A biologically defined exposure scale for the comparative description of rocky shores. Field Studies 1: 1 - 19 [altered pagination].

BOCQUET, C.; LÉVI, C.; TEISSIER, G. 1951: Recherches sur le polychromatisme de Sphaeroma serratum (F.). Archs Zool. exp. gén. 87: 245 - 297.

BROEKHUYSEN, G.J. 1940: A preliminary investigation of the importance of desiccation, temperature and salinity as factors controlling the vertical distribution of certain intertidal marine gastropods in False Bay, South Africa. Trans. R. Soc. S. Afr. 28: 255 - 292.

BULLOCK, T.H. 1958: Homeostatic mechanisms in marine organisms. Pp. 199-210 in Buzzati-Traverso, A.A. (ed.), 'Perspectives in Marine Biology'. University of California Press, Berkely and Los Angeles.

CHILTON, C. 1882: Further additions to our knowledge of the New Zealand Crustacea. Trans. N.Z. Inst. 15: 69 - 86.

_____ 1882: On two new Isopods. Trans. N.Z. Inst. 15: 188 - 190.

CHILTON, C. 1909: The Crustacea of the Subantarctic Islands of New Zealand. Pp. 601 - 671 in Chilton, C. (ed.), 'The Subantarctic Islands of New Zealand'. Government Printer, Wellington, Vol. 2.

DAHL, E. 1948: On the smaller Arthropoda of marine algae, especially in the polyhaline waters off the Swedish west coast. Undersökningar över Öresund 35, 193 pp. Lund.

DANA, J.D. 1853: Crustacea. U.S. explor. Exped. 14: 690 - 1018.

DAVIDSON, J. 1944: On the growth of insect populations with successive generations. Aust. J. exp. Biol. med. Sci. 22: 95 - 103.

DEARBORN, J.H. 1967: Food and reproduction of Glyptonotus antarcticus (Crustacea : Isopoda) at McMurdo Sound, Antarctica. Trans. R. Soc. N.Z., Zool. 8: 163 - 168.

DOBZHANSKY, T. 1951: Genetics and the origin of species. Columbia University Press, New York. Pp. x, 364.

GOUDEAU, Marie 1966: Génétique des populations de Sphaeroma serratum (F.). VIII. - Nouvelles observations sur la stabilité du polychromatisme local. Cah. Biol. mar. 7: 251 - 258.

HALE, L.J. 1958: Biological laboratory data. Methuen, London. 147 pp.

HANSEN, J.J. 1905: On the propagation, structure, and

classification of the Sphaeromidae. Q. Jl microsc. Sci. 49: 69 - 135.

HURLEY, D.E. 1956: The New Zealand species of Iais (Crustacea Isopoda). Trans. R. Soc. N.Z. 83: 715 - 719.

_____ 1961: A checklist and key to the Crustacea Isopoda of New Zealand and the Subantarctic Islands. Trans. R. Soc. N.Z., Zool. 1: 259 - 292.

JENSEN, J.P. 1955: Biological observations on the isopod Sphaeroma hookeri Leach. Vidensk. Meddr dansk naturh. Foren. 117: 305 - 339.

KINNE, O. 1954: Eidonomie, Anatomie und Lebenzyklos von Sphaeroma hookeri Leach (Isopoda). Kieler Meeresforsch. 10: 100 - 120.

_____ 1963: The effects of temperature and salinity on marine and brackish water animals. I. Temperature. Oceanogr. mar. Biol. 1: 301 - 340.

_____ 1964: The effects of temperature and salinity on marine and brackish water animals. II. Salinity and temperature salinity combinations. Oceanogr. mar. Biol. 2: 281 - 339.

MAYR, E. 1963: Animal species and evolution. Belknap Press of the Harvard University Press, Cambridge, Massachusetts. Pp. xiv, 797.

MENZIES, R.J. 1962: The zoogeography, ecology, and systematics of the Chilean marine isopods. Rep. Univ. Lund Chile Exped. 1948-49, 42: 1 - 162.

MILNE EDWARDS, H. 1840: Histoire naturelle des Crustacés. Libraire Encyclopédique de Boret, Paris. 3 v., 638 pp.; Atlas, 32 pp. 42 pls.

MOORE, H.B. 1958: Marine Ecology. John Wiley, New York. Pp. xi, 493.

NAYLOR, E. 1955a: The ecological distribution of British species of Idotea (Isopoda). J. Anim. Ecol. 24: 255 - 269.

_____ 1955b: The life cycle of the isopod Idotea emarginata (Fabricius). J. Anim. Ecol. 24: 270 - 281.

_____ 1955c: The diet and feeding mechanism of Idotea. J. mar. biol. Ass. U.K. 34: 347 - 355.

_____ 1955d: The comparative external morphology and revised taxonomy of the British species of Idotea. J. mar. biol. Ass. U.K. 34: 467 - 493.

PFEFFER, G. 1881: Die Krebse von Süd-Georgien nach der Ausbeute der Deutschen Station 1882-83. I. Teil. Jahrb. der Hamburg Wissensch. Anstalten 4: 43 - 150.

RASMUSSEN, R.A. 1965: The intertidal ecology of the rocky shores of the Kaikoura Peninsula. Ph.D. Thesis. University of Canterbury, Christchurch.

RICHARDSON, H.E. 1906: Descriptions of new isopod crustaceans of the family Sphaeromidae. Proc. U.S. natn. Mus. 31: 1 - 22.

RIEGEL, J.A. 1959: Some aspects of osmoregulation in two species of sphaeromid isopod crustacea. Biol. Bull. mar. biol. Lab., Woods Hole 116: 272 - 284.

SIMPSON, G.G.; ROE, A.; LEWONTIN, R.C. 1960: 'Quantitative zoology'. Rev. ed. Harcourt Brace, New York. Pp. vii, 440.

SJÖBERG, Birgitta 1967: On the ecology of the Jaera albifrons group (Isopoda). Sarsia 29: 321 - 348.

THOMSON, G.M. 1878: New Zealand Crustacea, with descriptions of new species. Trans. N.Z. Inst. 11: 230 - 248.

THORSON, G. 1946: Reproduction and development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound (Øresund). Meddr. Kommn. Havunders Kbh., Ser. Plankton, Bd. 4, pp. 1 - 523.

TODD, Mary E. 1963: Osmoregulation in Ligia oceanica and Idotea granulosa. J. exp. Biol. 40: 381 - 392.

WEST, D.A. 1964: Polymorphism in the isopod Sphaeroma rugicauda. Evolution 18: 671 - 684.

WIESER, W. 1959: Free living nematodes, IV. - General part. Rep. Univ. Lund Chile Exped. 1948-49, 34: 1 - 203.

WILSON, D.P. 1951: A biological difference between natural sea waters. J. mar. biol. Ass. U.K. 30: 567 - 579.

_____ 1952: The influence of the nature of the substratum on the metamorphosis of the larvae of marine animals, especially the larvae of Ophelia bicornis Savigny. Annls Inst. oceanogr., Monaco 27: 49 - 156.